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25.—BIOLOGICAL STUDIES OF *APHIS RUMICIS* L. A.—Appearance of Winged Forms. B.—Appearance of Sexual Forms. By J. Davidson, D.Sc. From the Entomological Department, Institute of Plant Pathology, Rothamsted Experimental Station, Harpenden, Herts. [Communicated by Professor G. H. Carpenter.]

26.—THE OCCURRENCE OF DEWALQUEA IN THE COAL-BORE AT WASHING BAY. By T. Johnson, D.Sc., F.L.S., Professor of Botany, Royal College of Science for Ireland, and Jane G. Gilmore, B.Sc. (Plates XI, XII.)

27.—A SIMPLE FORM OF APPARATUS FOR OBSERVING THE RATE OF REACTION BETWEEN GASES AND LIQUIDS, AND ITS USE IN DETERMINING THE RATE OF SOLUTION OF OXYGEN BY WATER UNDER DIFFERENT CONDITIONS OF MIXING. By H. G. Becker, A.R.C.Sc.I., A.I.C., Demonstrator in Chemistry, Royal College of Science, Dublin.

28.—THE OCCURRENCE OF A SEQUOIA AT WASHING BAY. By T. Johnson, D.Sc., F.L.S., Professor of Botany, Royal College of Science for Ireland, and Jane G. Gilmore, B.Sc. (Plates XIII, XIV.)

29.—THE SOURCES OF INFECTION OF POTATO TUBERS WITH THE BLIGHT FUNGUS, *PHYTOPHTHORA INFESTANS*. By Paul A. Murphy, B.A., A.R.C.Sc.I., Assistant in the Seeds and Plant Disease Division, Department of Agriculture and Technical Instruction for Ireland.

[Authors alone are responsible for all opinions expressed in their Communications.]

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uranium. The difference is probably, however, one of size, as in the initial stages of recovery the particles emitted may not be so large as they become after a prolonged period of rest.

Nuclei of a different type are emitted at glowing temperatures. In this case the glass does not become fatigued, and the nuclei are probably produced by the decomposition of the glass itself.

III.

When platinum wires are heated electrically, nuclei are driven off before the wire begins to glow. This emission lasts only a short time, just as in the case of glass, and is probably due to occluded impurities.

When these impurities are driven off by heat, the wire emits no nuclei until it begins to glow. The emission at glowing temperatures is very constant, and does not fatigue. The size and number of the nuclei emitted increase with the temperature.

Similar results were obtained with a wire of ni-chrome, an alloy of nickel and chromium.

Thus in all cases examined where nuclei are driven off from a substance by heat an initial emission takes place at low temperatures which falls off rapidly. The emission of nuclei when the substance glows is practically constant.

XXV.

BIOLOGICAL STUDIES OF *APHIS RUMICIS* L.

A.—Appearance of Winged Forms.
B.—Appearance of Sexual Forms.

By J. DAVIDSON, D.Sc.
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(COMMUNICATED BY PROFESSOR G. H. CARPENTER.)

[Read April 26. Published August 29, 1921.]

CONTENTS.

	PAGE
I. Introduction and Experimental Data.	
(a) Fundatrix generation on Euonymus,	305
(b) The First viviparous generation on Euonymus,	305
(c) Successive viviparous generations on Euonymus,	305
(d) Successive viviparous generations on Rumex,	307
(e) Successive viviparous generations on Beans,	308
(f) Euonymus infected from Beans,	309
II. General Discussion.	
(A) Appearance of winged forms,	310
(B) Appearance of sexual forms,	315
III. Summary,	321
IV. References,	322

I.—Introduction and Experimental Data.

The results embodied in this paper have been derived from extensive breeding experiments with this species in captivity during 1913-14 in Germany and 1920 at Rothamsted. Ova were found on March 25th, 1914, and were hatched out in the laboratory, the Fundatrices being transferred to small *Euonymus* bushes, *Rumex* plants, etc., which were grown in pots, and kept covered with muslin bags. As each succeeding generation became adult, some of the offspring were transferred to new plants. In this way the history of the aphids used was known, and the exact generation with which the various plants were infected. Unfortunately, for the 1920 experiments ova could not be found, so that the colonies in these experiments were started from an early, viviparous, parthenogenetic generation found on *Euonymus europaeus* on the Rothamsted farm on May 10th, 1920.

The plants were grown in 10″ pots in a large open glass-house in summer, and a warm green-house in winter. The daily maximum and minimum temperature of the green-house throughout the winter is shown in fig. 2.

I wish to express my thanks to Dr. A. D. Imms for the helpful suggestions he has given me during the progress of the experiments, and to Mr. Ward Cutler for his criticism when writing the paper.

(a) *Fundatrix Generation on Euonymus.*

Young aphids (1st instar), which hatched out from ova of *Aphis rumicis*, from *Euonymus*, were reared on young twigs of *Euonymus europaeus*, which were kept in wet sand in the laboratory. They all developed into a.v. ♀ ♀, being the adult Fundatrices.

In six experiments it was found that Fundatrices became adult in 8 to 10 days after birth, and commenced to produce young within 2 to 4 days after the last moult. The young in all cases were apterous viviparous females.

(b) *The First Viviparous Generation on Euonymus europaeus.*

The offspring of the Fundatrices are the first viviparous generation. In these experiments, individuals of the first viviparous generation born between April 13th and 18th, 1914, became adult in 9–11 days after birth. In all cases they gave rise to a.v. ♀ ♀, and the first young were produced in seven instances on the same day that the last moult took place. In the remaining cases, the first young were produced in 1 to 3 days after the last moult. They were grown on twigs of *Euonymus* in wet sand.

(c) *Successive Viviparous Generation reared on Euonymus.*

Small *Euonymus* bushes, about a foot high, were grown in pots and infected as required, each plant being covered with a muslin bag. Observations were made as recorded below. It should be noted that when winged forms are transferred to a new plant there is often great difficulty in getting them to settle down on the plant, and several days may elapse before they produce young on it. Sometimes, out of as many as fifteen winged forms, only two or three will settle down and produce on the plant, the remainder collecting in the top of the muslin cover. By restricting the space round the plant, this difficulty can be somewhat overcome.

Euonymus A.—11. 4. 14. Infected with two Fundatrices reared from ova on Euonymus. 23. 4. 14. Adult w. v. ♀ ♀ present; only a few a. v. ♀ ♀ present.

Euonymus A_1.—23. 4. 14. Infected with 4 w. v. ♀ ♀, 1st v. gen. from A. 12. 5. 14. Plant is not making young growth and is "woody." Aphids small size, restless, and wandering over the plant; some immature w. v. ♀ ♀ present, but majority are a. v. ♀ ♀, some a. v. ♀ ♀ adult.

Euonymus A_2.—25. 4. 14. Infected with 3 w. v. ♀ ♀, 1st v. gen. from A.

8. 5. 14. 2nd v. gen. are all a. v. ♀ ♀, large size, dull black in colour, with parts of legs and antennae yellowish white in contrast; the plant making young growth. 24. 5. 14. Plant heavily infested, aphids small size, many w. v. ♀ ♀ present.

Euonymus A_3.—27. 4. 14. Infected with 2 a. v. ♀ ♀, 1st v. gen. from A. 18. 5. 14. Plant is not making young growth; aphids small size; majority are w. v. ♀ ♀, only 3 a. v. ♀ ♀ present.

Euonymus A_4.—12. 5. 14. Infected with 5 a. v. ♀ ♀, 2nd v. gen. from A_1. 24. 5. 14. 3rd v. gen. are a. v. ♀ ♀ and w. v. ♀ ♀.

Euonymus A_5.—10. 5. 14. Infected with 3 a. v. ♀ ♀, 2nd v. gen. from A_2. 24. 5. 14. 3rd v. gen. practically all w. v. ♀ ♀; plant has young growth.

Euonymus A_6.—24. 5. 14. Infected with 4 w. v. ♀ ♀, 3rd v. gen. from A_5. 10. 6. 14. 4th v. gen. small numbers but large size, all a. v. ♀ ♀, some adult.

Euonymus A_7.—10. 6. 14. Infected with 8 a. v. ♀ ♀, 4th v. gen. from A_6. 20. 6. 14. Some aphids of 5th v. gen. are adult; all are w. v. ♀ ♀; plant has young growth.

Euonymus A_8.—20. 6. 14. Infected with 6 w. v. ♀ ♀, 5th v. gen. from A_7. 26. 6. 14. All the w. v. ♀ ♀ have died without producing any young. Reinfected with 8 w. v. ♀ ♀ from A_7. 6. 7. 14. About 20 aphids 6th v. gen. produced; killed off the winged mothers. 15. 7. 14. 6th v. gen. not yet adult; very small size; plant not making young growth; transferred the aphids to a new plant. 23. 7. 14. Some of the aphids now adult; all are a. v. ♀ ♀ small size; plant is not making young growth. 30. 7. 14. Aphids very small size; plant woody; several aphids of 7th v. gen. produced.

Owing to the unavoidable termination of the "A" series in July, 1914, the experiments were continued during the summer of 1920. As it was not possible to find ova of *Aphis rumicis*, the experiments were started with an early apterous viviparous generation found on *Euonymus europaeus* on 10th May, 1920. Winged forms were present, so it might be presumed that these were probably the second viviparous generation after Fundatrices. Allowing ten days for development of each generation, this would mean that the eggs hatched about April 10th.

Small *Euonymus* trees grown in pots and covered with muslin bags were infected as recorded below. By "cutting back" the bushes, young growth was obtained throughout the summer.

Euonymus E_1.—10. 5. 20. Infected with two a. v. ♀ ♀ from Euonymus europaeus. 15. 7. 20. Plant heavily infested.

Euonymus E_2.—15. 7. 20. Infected with 8 a. v. ♀ ♀ from Euonymus E_1. 28. 7. 20. About 30 aphids produced, big and healthy; plant has young growth. 10. 8. 20. Many winged forms produced; a few ♂ ♂ present.

Euonymus E_3.—18. 8. 20. Infected with a. v. ♀ ♀ and winged forms from Euonymus E_2. 24. 8. 20. A. v. ♀ ♀ producing young; only one winged form producing, remainder will not settle on the plant. 31. 8. 20. Only a few Aphids on the plant, small size, apterous. 14. 10. 20. The plant is shedding its leaves; a good number of aphids present; small size; many winged forms; ♂ ♂ and sexual ♀ ♀ present.

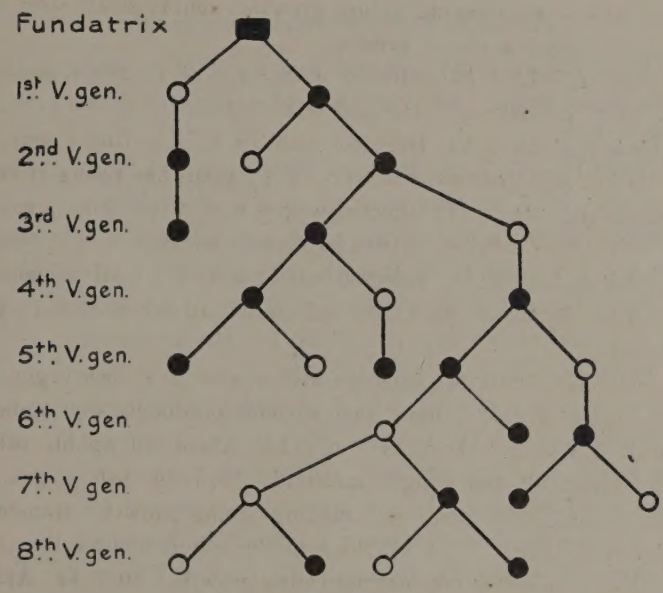

FIG. 1.

Table illustrating appearance of winged and apterous forms of Aphis rumicis on Rumex. 1st v. gen., etc., = 1st viviparous generation; ● = a.v. ♀ ♀; O = w.v. ♀ ♀.

(d) *Successive Viviparous Generations reared on Rumex.*

Rumex plants were grown in pots and infected with a. v. ♀ ♀ and w. v. ♀ ♀ respectively, in the different generations.

The first infection was to Rumex No. 1 with one Fundatrix of *Aphis rumicis* from *Euonymus europaeus* on 13. 4. 14.

The last infections were Rumex Nos. 16 and 17 with w. v. ♀ ♀ and a. v. ♀ ♀ respectively, of the 7th v. gen. from Rumex No. 14 on 16. 7. 14.

The aphids made rapid progress, and were usually of large size and dull olive green colour.

In some generations only apterous forms were produced, although winged forms always appeared in later generations, when the aphids were left to reproduce on the plant.

The appearance of the winged and apterous forms is shown in fig. 1.

It must be noted, however, that, owing to technical difficulties, where so many breeding cages are under observation, it is not possible to breed out all the offspring. The table below must therefore be taken as only expressing the general trend of the appearance of winged and apterous viviparous females.

(e) *Successive Generations of Aphis rumicis on Broad Beans.*

(Variety: Sutton's Prolific Longpod.)

Broad Beans B.—16. 6. 20. Infected with 2 a. v. ♀ ♀; offspring of winged migrants on Broad Beans. 12. 7. 20. A large number of aphids present, a. v. ♀ ♀ and w. v. ♀ ♀.

Broad Beans B_1.—10. 7. 20. Infected with 4 a. v. ♀ ♀ from B. 19. 7. 20. Offspring adult. 26. 7. 20. One adult w. v. ♀ ♀, remainder a. v. ♀ ♀, large size, infestation heavy; killed off the plant and infected a new plant with four of the a. v. ♀ ♀. 10. 8. 20. Many a. v. ♀ ♀ and w. v. ♀ ♀ present.

Broad Beans B_2.—10. 7. 20. Infected with 4 w. v. ♀ ♀ from B. 19. 7. 20. Some a. v. ♀ ♀ adult, large size. 26. 7. 20. Infestation heavy.

Broad Beans B_3.—25. 7. 20. Infected with 6 a. v ♀ ♀ from B_2. 4. 8. 20. A. v. ♀ ♀ and w. v. ♀ ♀ present. 12. 8. 20. Many winged forms present.

Broad Beans B_4.—6. 8. 20. Infected with 6 a. v. ♀ ♀ from B_3. 27. 8. 20. Infestation heavy, a. v. ♀ ♀ and w. v. ♀ ♀ present; killed off plant and infected a new plant with some of the apterous and winged forms. 14. 9. 20. Many a. v. ♀ ♀ and w. v. ♀ ♀ present; killed off the new plant.

Broad Beans B_5.—14. 9. 20. Infected with 5 a. v. ♀ ♀ from B_4. 11. 10. 20. A. v. ♀ ♀; w. v. ♀ ♀, a few ♂ ♂, and two sexual ♀ ♀ present.

Broad Beans B_6.—11. 10. 20. Infected with 10 a. v. ♀ ♀ from B_5. 29. 10. 20. A few a. v. ♀ ♀, many w. v. ♀ ♀, and several ♂ ♂ present. Development slow owing to low temperature in glass-house.

NOTE.—From B_7 onwards the plants were kept in a warm green-house, the temperature varying as shown in chart, text (fig. 2).

Broad Beans B_7.—29. 10. 20. Infected with 5 a. v. ♀ ♀ from B_6. 18. 11. 20. 3 w. v. ♀ ♀ adult, many immature winged forms, large size (sexuparae alatae). 26. 11. 20. All the aphids are w. v. ♀ ♀ (sexuparae), and a few ♂ ♂.

Broad Beans B_8.—23. 11. 20. Infected with one of the a. v. ♀ mothers on B_7. 5. 12. 20. Four w. v. ♀ ♀ and one a. v. ♀ produced. Allowed w. v. ♀ ♀ to produce on the same plant. 26. 12. 20. The w. v. ♀ ♀ have produced oviparous ♀ ♀.

Broad Beans B_9.—(Two plants.) Infected one plant on 19. 11. 20, and the other on 25. 11. 20, each with one w. v. ♀ from B_7. Only sexual ♀ ♀ produced in each case; hence these are true female-producing sexuparae.

They produced 11 and 22 females respectively, which were adult on 5. 12. 20 and 9. 12. 20. A third w. v. ♀ produced only sexual ♀ ♀.

Broad Beans B_{10}.—5. 12. 20. Infected with a. v. ♀ from B_8. 23. 12. 20. One a. v. ♀ produced, remainder are w. v. ♀ ♀; total 20.

Broad Beans B_{11}.—1. 12. 20. Infected with 10 w. v. ♀ ♀ from B_7. 26. 12. 20. All the aphids produced are sexual ♀ ♀.

Broad Beans B_{12}.—23. 12. 20. Infected with the one a. v. ♀ from B_{10}. 9. 1. 21. Offspring consists of 10 w. v. ♀ ♀ adult, 2 adult a. v. ♀ ♀, and remainder nymphs of winged forms; some ♂ ♂.

Broad Beans B_{13}.—26. 12. 20. Infected with 10 w. v. ♀ ♀ from B_{10}. 1. 1. 21. Four w. v. ♀ ♀ have produced young. 12. 1. 21. All offspring are oviparous ♀ ♀; some are adult.

Broad Beans B_{14}.—10. 1. 21. Infected with 2 a. v. ♀ ♀ from B_{12}. 5. 2. 21. w. v. ♀ ♀ (sexuparae), ♂ ♂, and 4 a. v. ♀ ♀ produced.

Broad Beans B_{15}—10. 1. 21. Infected with 5 w. v. ♀ ♀ from B_{12}. 24. 1. 21. 18 oviparous ♀ ♀ produced.

Broad Beans B_{16}.—24. 1. 21. Infected with 4 a. v. ♀ ♀ from B_{14}. 3. 2. 21. 3 ♂ ♂; several w. v. ♀ ♀ and 1 a. v. ♀ produced.

Broad Beans B_{17}.—5. 2. 21. Infected with 5 w. v. ♀ ♀ from B_{14}. 21. 2. 21. Only one w. v. ♀ reproduced, and gave 6 oviparous ♀ ♀.

Broad Beans B_{18}.—3. 2. 21. Infected with the 5 a. v. ♀ ♀ from B_{16}. 23. 2. 21. 2 a. v. ♀ ♀; several ♂ ♂; several w. v. ♀ ♀ present. 19. 2. 21. The 5 original a. v. ♀ mothers put on a new plant, and on 2. 3. 21 they had produced 3 a. v. ♀ ♀, some ♂ ♂, and w. v. ♀ ♀.

Broad Beans B_{19}.—23. 2. 21. Infected with 5 w. v. ♀ ♀ from B_{18}. 10. 3. 21. All oviparous ♀ ♀ produced.

Broad Beans B_{20}.—2. 3. 21. Three plants infected each with one a. v. ♀ from B_{18}. 26. 3. 21. 5 a. v. ♀ ♀, one ♂, and 40 w. v. ♀ ♀ produced.

(f) *Euonymus Europaeus Infected from Broad Beans.*

Euonymus E_6.—16. 6. 20. Infected with a. v. ♀ ♀, offspring of winged migrants on Broad Beans. 29. 6. 20. Many aphids present, mostly a. v. ♀ ♀, but some w. v. ♀ ♀.

Euonymus E_7.—10. 7. 20. Infected with 25 w. v. ♀ ♀ from Beans B. 18. 7. 20. Many colonies produced beneath the leaves. 5. 8. 20. Aphids small size, dark colour, many winged forms; infestation heavy; plant has no young growth.

Euonymus E_8.—19. 8. 20. Infected with 15 w. v. ♀ ♀ from Beans B_4. 31. 8. 20. Many aphids produced, some adult a. v. ♀ ♀ 14. 9. 20. Plant heavily infested; many aphids wandering over the plant and muslin cover.

14. 10. 20. Plant shedding its leaves; a. v. ♀ ♀, w. v. ♀ ♀, ♂ ♂ and sexual ♀ ♀ present; ova laid.

Euonymus E_9.—14. 9. 20. Infected with 15 w. v. ♀ ♀ from Beans B_4. This plant has a lot of young growth. 14. 10. 20. Many aphids present; ♂ ♂ and sexual ♀ ♀ present.

Euonymus E_{10}—11. 10. 20. Infected with 10 w. v. ♀ ♀ from Beans B_5. 14. 10. 20. Only two winged forms producing on the plant. 30. 10. 20. Offspring now adult, all sexual ♀ ♀, 16 in number.

Euonymus E_{11}.—(Kept in warm greenhouse.) 24. 11. 20. Infected with one w. v. ♀ from Beans B_7. 9. 12. 20. Offspring all oviparous ♀ ♀, 24 in number, some adult. 26. 12. 20. Ovip. ♀ ♀, large size; no ova produced.

Euonymus E_{12}.—25. 2. 21. Infected with one w. v. ♀ (sexupara) from Beans B_{18}. 12. 3. 21. Only oviparous ♀ ♀ produced, some nearly adult. 12. 4. 21. All the oviparous ♀ ♀ alive, have distended abdomen; no ova laid. Ova in the bodies, but females not fertilized.

II.—General Discussion.

A.—*Appearance of Winged Forms.*

It was almost universally held by the earlier investigators who studied the biology of Aphids that poor sap conditions obtaining in plants resulted in the production of winged forms. Later investigations indicated that temperature and humidity may also be important factors.

The results obtained by these earlier workers have been so often reviewed in the literature on Aphids that it seems unnecessary to review them again.

Starting therefore with Mordwilko (1907–1909), who in his extensive observations on the biology of Aphids gives a general idea of the views obtaining at that time, we see that food conditions, probably correlated with temperature, were accepted as the important factors.

Investigations during the next few years on the life cycle of Aphids from the cytological aspect lead one to the view that, although external factors may have some influence on the production of winged forms, there is in all probability some internal inherent mechanism at work which is the important factor.

Later results obtained from breeding experiments, notably by Klodnitzki (1912), Baker and Turner (1916), and Matheson (1919), in which winged forms were obtained in many of the parthenogenetic generations, would seem to support this view. The situation at present is, however, by no means clear, and external influences, especially of food and temperature, would appear to be very important factors in the results obtained by some recent workers, notably Ewing (1916) and Shinji (1918). In discussing this

question further, however, I hope to show with reference to the results of my experiments that those obtained by the latter authors are by no means conclusive.

Ewing, working with *Aphis avenae* Fab., considers temperature is the determining factor. The optimum temperature of 65° F. resulted in only apterous forms being produced during 20 parthenogenetic generations.

Klodnitzki obtained winged forms along with apterous forms in most generations when breeding the dark green and brown varieties of *Siphonophora* (Macrosiphum) *rosae* Koch, in normal and abnormally low temperatures. Similarly with *Aphis hederae* Kalt., over 35 agamic generations, winged forms appeared in low temperatures as in normal temperatures. There was a tendency for a. v. ♀ ♀ to produce winged forms.

Shinji investigated the influence of food conditions on the production of winged forms in Aphids. By growing cut stems of plants infected with aphids, in sand moistened with solutions of certain chemical substances, he obtained results which suggest that the percentage of winged forms produced was influenced. This was especially the case with solutions of Mg. sulphate.

The figures obtained are interesting, but a further investigation of the subject is desirable. It is necessary to know the history of the Aphids experimented with, and the number of the viviparous generation used. Comparisons between the effect on the offspring of w. v. ♀ ♀ and a. v. ♀ ♀ respectively should be observed. The varying individuality of the Aphids concerned, relative to an inherent tendency to wing development, should be known. Temperature and humidity factors must also be considered.

It will be seen in my experiments that winged forms appeared in most of the generations. Winged viviparous females produced as a rule only apterous viviparous females, although in one or two cases (see text, fig. 1) a few winged forms developed as well as apterous forms. Apterous viviparous females, offspring of w. v. ♀ ♀, usually produced a varying percentage of winged forms, although sometimes only a. v. ♀ ♀ were produced. This sequence was the same on different species of plants.

Winged forms have been obtained on young succulent shoots of *Euonymus europaeus* and apterous forms on "woody," non-succulent plants.

Food conditions, therefore, would appear not to be the deciding factor. The tendency appears to be for a. v. ♀ ♀ to produce a mixed progeny of w. v. ♀ ♀ and a. v. ♀ ♀, or in some cases only a. v. ♀ ♀. W. v. ♀ ♀, on the other hand, invariably produce a. v. ♀ ♀, with only occasionally winged forms in later generations. It is seen that when a plant, either the winter host (*Euonymus*), or an intermediate host (Beans), is infected, either with a. v. ♀ ♀ or w. v. ♀ ♀, and the Aphids allowed to reproduce freely on the

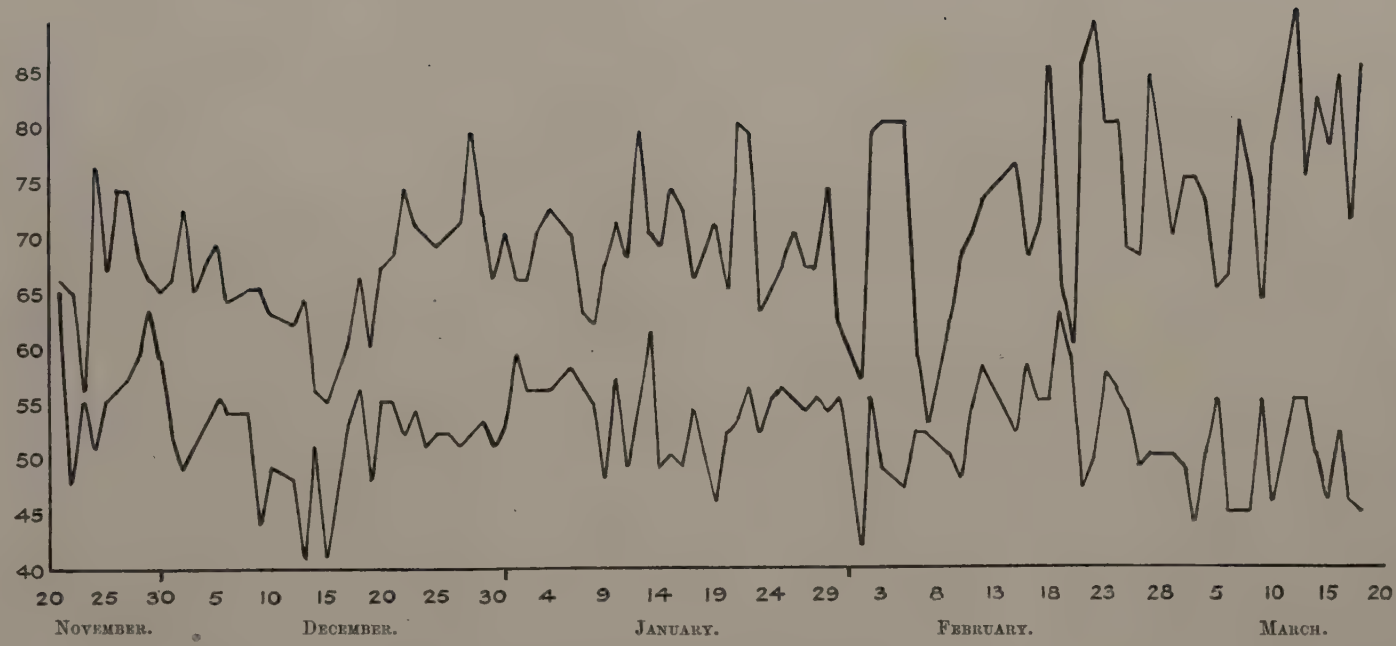

Fig. 2.

Temperature Chart of Green-house, November 21st, 1920, to March, 1921.

Upper line shows maximum daily temperature.
Lower line shows minimum daily temperature.

plant, winged forms always appear in due course. Although at the time that winged forms appear in great numbers the plant may be heavily infested, the appearance of the winged forms is not necessarily connected with the condition of the plant, but due to the innate tendency of the apterous females to produce winged forms as described above. It would seem that the overlooking of this fact has clouded the observations of earlier observers, who correlated the conditions of the plant with the appearance of winged forms.

The sequence of the development of winged forms on *Rumex*, *Euonymus* and Beans is well shown in figs. 1 and 3.

The percentage of winged forms which may develop in any generation as offspring of a. v. ♀ ♀, varies considerably.

The tendency for a higher percentage of winged forms to develop in some cases on Sugar Beet, Red Beet, and Poppies, and also on some varieties of Broad Beans, has been observed in my experiments.[1] It is not at all clear, however, that this can be considered as due to the nature of the cell sap of the different plants acting on the Aphid metabolism. Owing to the wide variation in the numbers of winged forms produced, it seems that factors other than food and temperature must be looked for.

In these experiments temperature and humidity varied, but the conditions were approximately the same for any series of experiments extending over the same period.

From my observations one is led to the view that the appearance of winged forms is determined by internal factors. It seems probable, however, that environmental conditions may exert an influence by restricting or favouring metabolism, and thus affecting the production of winged forms; but further experimental investigations in relation to temperature, humidity, and food factors and further cytological studies are necessary.

It seems to the author that the methods adopted for breeding Aphids may largely account for the conflicting results obtained by various workers. When one considers the number of offspring that an Aphid mother can produce, it is obvious that only an extremely small percentage of the Aphids in any generation can be isolated to carry on further generations.

From general observations on the progress of *Aphis rumicis* in colonies, there is a clearly indicated tendency for apterous viviparous females to eventually produce some winged forms. This inherent tendency may be more developed in some strains than in others, and a big element of chance occurs in the selection of Aphid mothers to carry on the generations.

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[1] *Vide* Davidson, J. (1921[a]).

Before one can investigate the influence of external factors on production of winged forms, it is necessary to estimate by extensive breeding experiments the extent and relations of this inherent tendency to wing-production

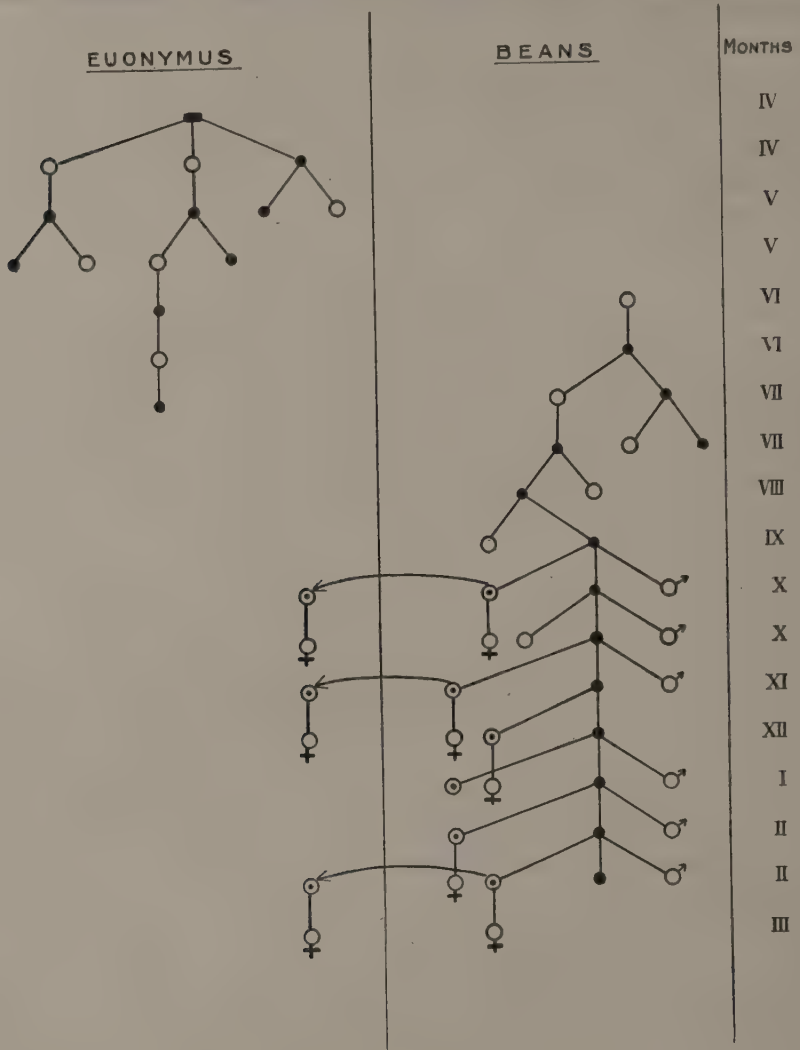


FIG. 3.

Illustrating, in successive generations of *A. rumicis*, the appearance of winged and apterous forms, also of sexual forms, on Broad Beans and Euonymus. The months are shown at the right-hand side. The series is being continued.

▬ Fundatrices. ● Apterous viviparous females. O Winged viviparous females. ⊙ Winged sexuparae. ♀ Sexual females. ♂ Males.

in different agamic females. It is generally considered that the winged condition is the more primitive, and that the apterous condition has arisen

later. In the loss of the wings, with the resulting change in body form, and in the loss of the sensoria on the antennae, is indicated a degeneration correlated with the more localized parasitic habits of the apterous form.

It seems to me therefore that external factors can only be considered as likely to exert an influence in restricting or favouring what is already present as an inherent tendency, and not in producing two complex dimorphic forms. Doubtless, external factors—food and climatic seasonal conditions—extending over long periods of time, have influenced the winged and apterous condition in the agamic generations.

(B).—*Appearance of Sexual Forms.*

The early conception of the alternation of sexual and parthenogenetic generations in the life cycle of Aphids was that external conditions—food and temperature—were the chief factors accounting for the appearance of the sexual forms and for bringing the parthenogenetic generations to an end. The experiments of several early workers, such as De Geer, Kyber, and others, whereby, with certain species of Aphids, parthenogenetic reproduction was continued for a great number of generations, under favourable food and temperature conditions, seemed to support this conception. Further, the view readily fitted in with general observations on Aphids in the field, namely, the widespread distribution of agamic females in the summer months and the occurrence of sexual forms in the autumn. Comparatively little experimental work on the *Aphididae* has been carried out, however; and the views held regarding Aphids are largely influenced by the results of the numerous researches on other animals, particularly the *Cladocera* and *Rotifera*, although in these cases sex appears to be largely determined by the chromosome complex.

The literature on this subject has been so frequently reviewed that it is not proposed to deal with it here.

With the development of the cytological aspect of the life cycle of the *Aphididae*, notably by Morgan, Stevens, Tanreuther, and von Baehr, it became clear that internal factors, closely associated with the chromosomes, must be considered of first importance. Whatever influence external factors may exert, they can hardly be considered as determining the sexual forms, although in the progress of adaptation and selection these factors have, doubtless, played an important part in favouring or restricting the parthenogenetic generations.

The more recent results obtained by breeding species of Aphids through several generations support the view that internal factors are the important ones concerned.

With individuals of some species, however, the parthenogenetic generations may be continued under favourable conditions for a long period, as has been shown in many cases. For example, Klodnitzki (1912) carried on agamic generations of *Siphonophora rosae var. glauca*, Buckton, for more than a year. Ewing (1916) carried on *Aphis avenae* for seventy-three parthenogenetic generations.

It would appear that in some species the sexual forms develop after a definite number of agamic generations have been passed through ; but this is not the case in all species, as is seen in my experiments and in those of Davis (1914) with *Callipterus trifolii*, Monell.

A further consideration is that, while certain individuals of the later summer agamic generations close the life cycle by producing only sexual forms, other individuals may also produce agamic females which continue the agamic generations under favourable conditions for a very long period. Klodnitzki carried on three cultures of *Aphis hederae* Kalt. over a number of generations. In two lines sexual forms appeared in the thirty-first generation, but no sexual forms appeared in the other line, even after forty-two generations had been passed through. Davis (1915) observed a similar agamic series in *Macrosiphum pisi* Kalt.

The continuation of parthenogenetic reproduction throughout winter under favourable conditions of food and temperature has been obtained in my experiments with *Aphis rumicis*. With the advent of unfavourable winter conditions in the field, the agamic generations would die off, but under mild conditions, and given a suitable food-plant, they may survive the winter, and slowly carry on the parthenogenetic reproduction.

The finding of a colony of agamic females of *Aphis rumicis* by Davidson (1914) on January 30th, 1913, on *Euonymus japonicus*, which, when brought into the green-house, continued agamic reproduction throughout 1913, would seem to support the latter view. This is an important consideration from the economic standpoint.

It is possible, of course, that some late parthenogenetic generations, delayed in their development on the approach of winter conditions, would normally under favourable conditions lead to sexual forms.

It appears that in Aphids the development of viviparous parthenogenetic generations, between the ova and the sexual forms, is an expression of adaptation and selection to environmental conditions, extending over the favourable seasons of the year.

Certainly in nature the approach of winter conditions would normally be the factor limiting the extent to which the parthenogenetic phase could be extended.

In this respect it is interesting to refer to the life cycle of *Aphis saliceti*, a species in which the number of parthenogenetic generations is very limited, the sexual forms appearing in early summer. As shown by Klodnitzki, the ova hatch out in April and May. Some of the Fundatrices produce ♂ ♂ and sexual ♀ ♀; others produce w. v. ♀ ♀, which migrate to other willow trees, and produce ♂ ♂ and sexual ♀ ♀.

Passing now to Aphis rumicis, it is seen that the agamic generations are further extended over the favourable seasons of the year. Normally in nature, the approach of winter conditions will be the important factor in bringing these agamic generations to an end.

In view of the cytological investigations in Aphids, it seems evident that some factor or factors associated with an adaptation of Aphids to seasonal conditions cause a radical change in chromozome segregation, resulting in the development of sexual forms, and the production of ova at a period which ensures the continuation of the species.

It seems feasible to expect that with an extension of favourable seasonal conditions, such as would obtain in a warmer climate, there would be a corresponding extension (due to adaptation) of the agamic generations. This appears to be the case in *Aphis avenae* Fabr., and *Toxoptera graminum* Rond. in America.

It is clear from my experiments that certain of the apterous, parthenogenetic females may carry on the parthenogenetic strain throughout winter if given favourable food and temperature conditions. This cannot, however, be considered as wholly due to these two factors, because sexual forms and agamic forms appear together in each generation under the same environmental conditions. It is, I think, just a case of parthenogenetic ♀ ♀, which normally on the secondary host-plants would have died off on the approach of unfavourable weather conditions, being saved by keeping them in a suitable environment.

One cannot say at present how far these cases occur in the *Aphididae*. It is highly probable that in breeding experiments, considering the very small percentage of the offspring used in each generation, it is only by chance that individuals are selected which have the continuing parthenogenetic tendency.

It is seen in the series Broad Beans B, B_1, B_2, &c., as illustrated in fig. 3, that parthenogenetic individuals were carried on Beans from May onwards throughout the winter. In winter the plants were kept in a warm green-house, and fresh Bean plants were raised in succession for each generation. Towards October, sexual forms appeared, and in some lines of the cultures the cycle closed by the production of these forms. Some of the

infected plants were put into the warm green-house with the hope of carrying on the agamic generations, and the interesting result shown in fig. 3 has been obtained. After October had set in, there was a marked tendency to production of sexual forms, and the agamic forms in most cases died out.

However, in the case illustrated in fig. 3 a few agamic a. v. ♀ ♀ developed, and these were isolated, and their offspring carefully watched. In each succeeding generation large w. v. ♀ ♀ (winged sexuparae, ♀ producers) and winged ♂ ♂ were produced; and in every case one or two agamic a. v. ♀ ♀ also developed, which were isolated to carry on the next generation. It was not possible to follow out the exact numbers of each form produced, owing to the great number of pots and plants that would be required; but winged sexuparae were in the majority, with a comparatively small number of ♂ ♂. The agamic a. v. ♀ ♀, on the other hand, were usually only one, two, or three in each of the later generations.

The development period of these agamic individuals is somewhat longer than that of the summer generations, and the numbers of offspring produced considerably less. This may to some extent be due to low concentration of the cell sap of the plants, owing to conditions of winter sunshine and reduced assimilation.

It will be seen that agamic and sexual forms in the same generations were obtained on Euonymus.

The females produced by the winged sexuparae grew well on Broad Beans, and became larger than normal females; but in no case were ova laid, although on dissecting these females several large eggs were found inside them. These ♀ ♀ in the experiments were not fertilized, owing to the fact that the Aphids were removed from the plants as they became adult.

In one case ten oviparous ♀ ♀, born on a Bean plant on 1st January, 1921, had not produced ova by 16th February, and by that time only two ♀ ♀ were alive. When some of the females were dissected, they were found to contain several large eggs.

Sexual forms were produced when the Aphids were kept continuously on *Euonymus europaeus*, and also when they were kept continuously on Beans.

As referred to in a previous paper (1921), sexual forms have been recorded in the field on *Rumex*, Sugar Beet, and Haricot Beans. It is evident, therefore, that the food plant in itself does not determine the appearance of the sexual forms. It is very interesting that sexual forms appear on the primary or secondary host, showing that the distribution of

winged migrants over a great number of intermediate hosts is not an essential part of the life-history, but must be regarded as an adaptation to a search for more suitable food conditions.

One cannot consider, therefore, that *Aphis rumicis* is a true migratory species on which the influence of the intermediate host is an essential part of the life cycle. If suitable conditions are available, the life cycle can be passed through on either the primary or the secondary host.

These conclusions, however, are largely based on the behaviour of Aphids in captivity. It is obvious, from the nature of the primary host and the temporary life of the secondary hosts, that the migration from the one to the other at suitable seasons is decidedly of benefit to the Aphids under natural conditions. It does not preclude, however, two very important possibilities in the life cycle of *Aphis rumicis* in nature, namely, (*a*) the occurrence of agamic females, which may continue under mild winter conditions, and carry on agamic reproduction in the following season; (*b*) the occurrence of sexual forms and winter eggs on plants other than *Euonymus europaeus*. These two possibilities may explain how, although one known winter host (*Euonymus europaeus*) of this species has a very localized distribution, the distribution of *Aphis rumicis* is a very wide one.

Unfavourable seasonal conditions over the period when sexuparae are being produced would result in a heavy mortality of the agamic forms, a reduction in the number of fertilized eggs laid, and a smaller outbreak of Aphids the following season.

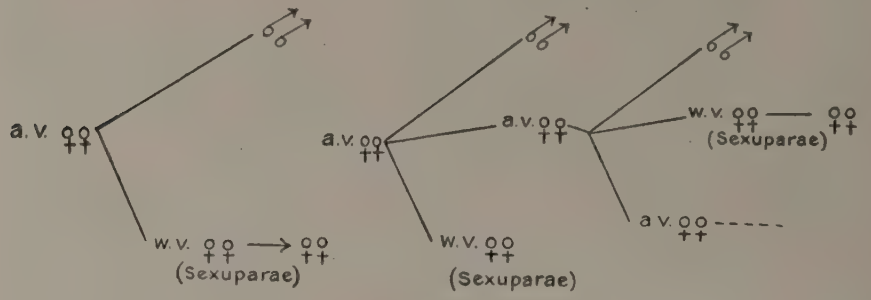
It has been shown that on the approach of autumn, the influence of some important factors results in the development of sexual forms irrespective of the number of the generation. There would appear to be at work some inherent tendency associated with adaptation to seasonal conditions. As autumn advances, an increased number of sexual forms appear.

♂ ♂ appeared on Euonymus E_2 on 10. 8. 20, and ♂ ♂ and sexual ♀ ♀ were present on Euonymus E_3 early in October. The sexual forms appeared also on Beans B_5 early in October. From September onwards an increasing number of sexual forms developed. In Beans B_{10} one agamic female continued parthenogenetic viviparous reproduction, giving rise to ♂ ♂, winged sexuparae and two a. v. ♀ ♀.

In my experiments the ♂ ♂ and oviparous ♀ ♀ were produced by different mothers, the winged sexuparae producing the oviparous females, and the a. v. ♀ ♀ (apterous sexuparae) producing the ♂ ♂.

The closing of the life cycle by the development of sexual forms

and the continuation of the agamic series may be shown in the following way :—



Klondnitzki found in *Aphis hederae* Kalt., that the sexuparae are apterous and the same mother produced both ♂ ♂ and ♀ ♀.

Baker and Turner (1916) found in *Aphis pomi* De Geer, that the same mother (sexuparae) could produce both sexes; and in one case a mother produced both sexes and agamic forms.

One can also consider in the case of *Aphis rumicis* that the same mother can give rise to both sexes, in that the winged sexuparae, which produce only sexual ♀ ♀, are presumably predestined in the original agamic mother to produce sexual ♀ ♀.

Similarly, both sexual and agamic forms are produced by the same mother.

From a colony of agamic apterous females—Beans B_5—all stages appeared in October, namely ♂ ♂, sexual ♀ ♀, a. v. ♀ ♀, and w. v. ♀ ♀.

In conclusion, it is seen that in my experiments sexual forms developed under favourable conditions of food and temperature. They may arise in different generations. They were produced under the low temperatures of October in the glass-house, and later under the warm temperature in the green-house. Further, agamic and sexual forms appeared together under the same conditions of food and temperature. The autumn seasonal factor would appear to be important in accounting for the large numbers of sexual forms produced at this period. It is difficult to believe that the influence of external factors is the important one, when one considers that under the same external conditions totally different forms are produced—namely, ♂ ♂, sexual ♀ ♀, and agamic females. Over long periods of time, external factors associated with seasonal conditions would be important, and it appears highly probable that the parthenogenetic and sexual phases are adaptations to seasonal conditions.

While the generative changes appear to be determined by an internal

mechanism associated with the chromosome complex, it seems feasible to expect that changes in the environment may, by influencing the metabolism of certain individuals, indirectly affect the natural sequence of chromosome segregation, and so affect sex-production.

This would allow of two conflicting views—internal mechanism and external factors—being brought into line, and would explain the result shown in figure 3.

External factors, therefore, may be regarded as exerting an influence by retarding, restricting, or favouring the appearance of sexual forms, and not as determining them.

III.—SUMMARY.

The early aphidologists considered that food and temperature conditions were the important factors influencing the apterous and winged forms in Aphids. This view appears to be upheld by the later experiments of Ewing and Shinji.

From cytological investigations on Aphids and recent breeding experiments, it appears highly probable that the sequence of winged and apterous forms is largely due to some internal, inherent tendency. W. v. ♀ ♀ tend to produce a. v. ♀ ♀, and a. v. ♀ ♀ to produce either a. v. ♀ ♀ or a mixed progeny, including a very variable percentage of winged forms. The apterous condition is to be regarded as an adaptation to seasonal food and temperature conditions. The great variability in the numbers of winged forms produced by apterous individuals is an important point to consider.

Similarly, food and temperature conditions were considered the important factors affecting the development of sexual forms. Later cytological investigations show that the appearance of the sexual forms is associated with changes in the chromosome complex. The agamic generations appear to be interpolated between the winter egg and the sexual generation as an adaptation to seasonal conditions. The approach of winter conditions would normally be the factor affecting the bringing to an end of the parthenogenetic phase and the appearance of the sexual forms.

In some cases the production of sexual forms may be superseded by continued parthenogenetic reproduction, certain agamic forms either reproducing slowly throughout a mild winter, or lying dormant and continuing reproduction the following season. In isolated cases, certain agamic individuals may be affected physiologically by some factor or factors acting on their metabolism, so that they do not respond to the inherent stimulus to develop into sexual forms. These individuals normally, in winter, would die, but under favourable conditions may continue agamic reproduction.

From the observations of other authors, however, it is evident that generalizations on the biology of the *Aphididae*, as a whole, cannot be drawn from the study of one species. Many special characteristics are exhibited by some species, owing to the complexity of the life cycle. Further investigations on the cytology of Aphids made in conjunction with breeding experiments are necessary for a clearer understanding of the biology of the *Aphididae*.

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XXVI.

THE OCCURRENCE OF DEWALQUEA IN THE COAL-BORE AT WASHING BAY.

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[Plates XI, XII.]

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In 1918 a boring to test the position of the concealed coalfield was begun by the Ministry of Munitions at Washing Bay, at the south-west corner of Lough Neagh. Owing to the unexpectedly enormous thickness of the beds of clay and basalt (1,500 feet instead of 250 feet estimated), the operations have been abandoned. The core has been placed in charge of the Geological Survey. Early in 1919 Mr. W. B. Wright, F.G.S., brought one of us pieces of the core containing plant remains for identification. For the past two years all available time has been devoted to the investigation of these remains, and many interesting results have been obtained.

We are indebted to Professor G. A. J. Cole, F.R.S., Director of the Geological Survey, for permission to examine the core, and to Mr. Wright for the following observations on the geological features of the district:—

"The boring put down by the Ministry of Munitions in the years 1918 and 1919 in search of the concealed coalfield supposed to exist beneath the Lough Neagh basin has yielded the first reliable evidence regarding the geological age of the Lough Neagh beds. The site selected was at Washing Bay, about four miles east of Coalisland, Co. Tyrone. The bore entered the Lough Neagh beds, beneath the glacial drift, at a depth of 48 feet, and reached the base of these beds at 1,196 feet 2 inches. The basal beds of the Lough Neagh series rested on about 70 feet of lithomarge produced by the decomposition of the Upper Basaltic lavas of Co. Antrim, which are well represented below. The series is, therefore, distintly post-basaltic in age, and is to be

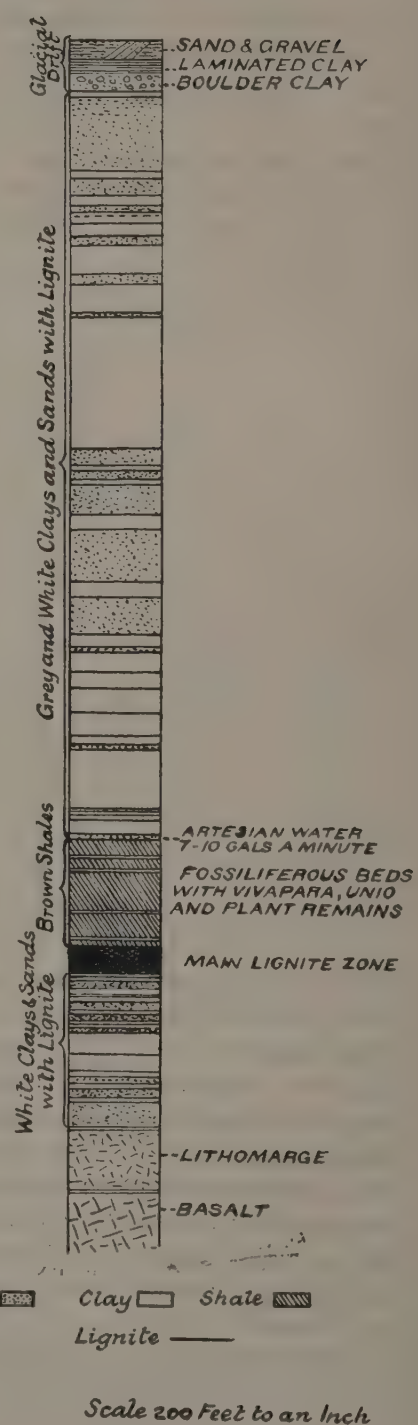
[1] Miss Gilmore's help was rendered possible by a grant from the Department of Industrial and Scientific Research.

referred to a later date than the plant-bearing beds of inter-basaltic age, which occur at Ballypallady. The Basaltic series of Co. Antrim rests as a whole on the chalk, which is of Upper Cretaceous age, and contains the zone of *Belemnitella mucronata.*

"The facts established by the boring, combined with certain relations observable at the surface and hitherto imperfectly understood, indicate with a fair amount of certainty that the Tertiary folding and faulting of the district affect equally the Lough Neagh beds and the lavas on which they rest. The earth movements which resulted in this folding and faulting are, for reasons which cannot be entered into here, generally considered to be of Miocene age. The Lough Neagh series is, therefore, presumably pre-Miocene. It is certainly not later than early Miocene.

"The stratigraphy of the Lough Neagh beds is exhibited in the accompanying diagram. The main horizons of identifiable plant remains occurred in the brown shales or clays between the depths of 881 feet and 1,008 feet 7 inches, lying mainly in the upper portions of these shales. The plant remains in the white clays above and below these beds were for the most part unidentifiable, being highly carbonized.

"From the geological relations alone it is impossible to draw any more exact conclusion regarding the



age of these beds than is embraced in the general statement that they come in somewhere between late Cretaceous and early Miocene times. As, however, the lake basin in which they were laid down was probably produced by some early forerunner of the Miocene earth-movement, there is a presumption in favour of the later portions of this long epoch.

" It is obvious that any palaeontological evidence that is obtainable becomes of very great importance in determining with more precision the horizon of the clays. Such a determination, moreover, would also assign an upper limit to the age of the great series of basaltic eruptions in north-eastern Ireland."

One of the most interesting fossils found in the coal-bore is the genus *Dewalquea.*

Our first recognized specimen occurs in the core at a depth of 903 feet, and reveals itself as a five-lobed leaf (Pl. XI, fig. 1) in all essential features, in agreement with the *Dewalqueas* of the European Continent and America. The whole leaf is 9 cm. long by 9 cm. broad ; the petiole being only partially preserved, is not included in the measurement. The petiole divides at its distal end into three branches, the two outer ones branching again. Each of the five branches carries a lanceolate, acuminate, toothed, coriaceous leaflet. The leaf is clearly compound, quinately palmate or pedate, not a simple palmatisect or pedatisect leaf. The medium leaflet is 8 × 1·5 cm., the inner lateral ones 7 × 1·5 cm., while the outer ones are much smaller, being 0·8 cm. wide, and probably only 4 cm. long. Neither leaflet of the outer pair is completely preserved in the specimen. The median petiolule is 3 mm. long, the lateral ones are 7 mm. long, and their branches very short. The base of the median leaflet is symmetrical and attenuated ; the bases of the others are asymmetrical. The base of each inner lateral leaflet has the lamina prolonged downwards on its inner side beyond the outer lamina, the converse being the case with the outer pair—clearly an adaptation of shape to space requirements. The edge of each leaflet is entire in its basal part, but serrate in the upper two-thirds of its length.

We have been able to restore the epidermis on both sides of the leaf. The upper and under epidermides (Pl. XII, figs. 5–8) consist of cells with more or less pronounced sinuous lateral walls. The lower epidermis shows numerous sinuous cuticular striae on the outer face of the cells. Similar striae are described by Nestler (1) in *Helleborus,* in which they are confined to the upper epidermis. The upper epidermis of our fossil shows minute cuticular tubercles like those on the under epidermis in *Helleborc.* Stomata are confined to the lower epidermis. They are 35–40μ in diameter, sub-circular in outline, without subsidiary cells. Peltate scales, circular

in outline, 60–76μ wide, and consisting of a shield of 6–8 cells on a short stalk, are frequent, and are observable even with the lens on the counterpart impression through becoming detached from the leaf-surface (Pl. XII, figs. 1–2). These peltate scales and the cuticular striae have not been found previously in *Dewalquea*, and must be taken into account in considering its systematic position.

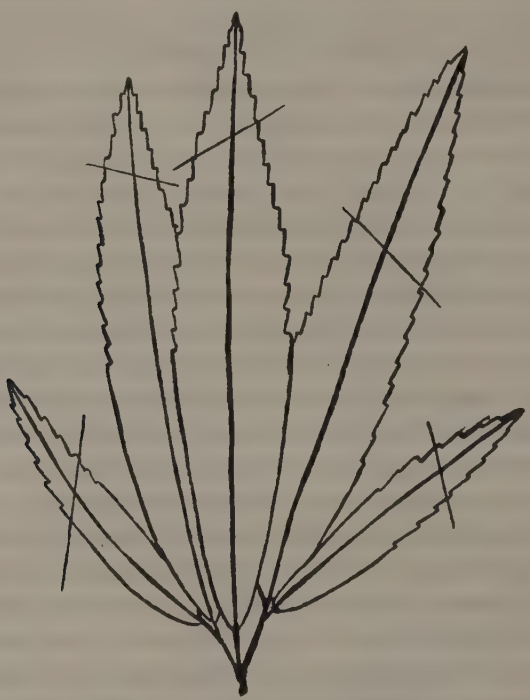


Fig. 1.—*Dewalquea hibernica* $\frac{2}{3}$ Restoration.

Fig. 2.—*D. fraxinifolia* $\frac{1}{1}$ Restoration.

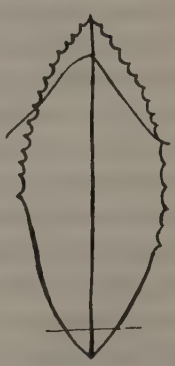


Fig. 3.—*D. denticulata* $\frac{1}{1}$ Restoration.

We propose to call the specimen just described *D. hibernica*. There are

many other examples of the genus in the core between 897–913 feet, as well as at 787 feet. One leaf shows three leaflets, and may be named *D. fraxinifolia* (Pl. XI, fig. 4). Another apparently simple leaf we propose to call *D. denticulata* (Pl. XI, fig. 11). Most of the other specimens—some twenty in all—are fragments of leaves only. They all show the *Dewalquea* type of tissue, and indicate that it was common in the locality.

Affinities of Dewalquea.

The discovery of *Dewalquea* was made by Debey in the Senonian (Upper Cretaceous) of Westphalia. He appears to have sent specimens and drawings to Saporta and Marion (2), then at work on the Belgian Tertiary flora, and also to Schimper (3). Debey's MS. name of *Araliophyllum*, accepted by Schimper, was not, however, adopted by Saporta and Marion, who replaced it by *Dewalquea* (after the Belgian geologist), three specimens being described—*D. haldemiana* S. and M. and *D. aquisgranensis* S. and M. from Westphalia, and *D. gelindenensis* S. and M. from the basal Eocene of Gelinden. Since 1874 other species have been described, of which Berry (4) gives a useful critical revision. They are all, with one exception, from the Upper Cretaceous, and are from America. One of the species, *D. Smithi*, is founded by Berry on material from the Tuscaloosa (Upper Cretaceous) beds of Alabama. *D. Smithi* is very similar to, but distinct from, *D. insignis* Hosius and von Marck from Haldem (Westphalia) (5). It differs from all previously recorded American species in being quinate, not ternate. It is similar to *D. coriacea* and *D. pentaphylla*, found by Velenovsky (6) in the Cenomanian of Bohemia. Knowlton (17), in 1917, described a second quinate specimen *D. pulchella*, which he considered closely allied to, if not identical with, *D. insignis* H. and von M. *Dewalquea* is an extinct type of leaf derivable from or of the same type as *Polytaenia quinquesecta* of the Turonian. It occurs in the Upper Cretaceous from Alabama to Greenland, in Westphalia and Bohemia, the Lower Eocene of Gelinden, in Belgium, and in the Oligocene of Italy. The recorded distribution in time and space adds considerably to the interest of the discovery of a *Dewalquea* in the coal-bore at Washing Bay. If the deposit be correctly referred to the Upper Oligocene, the Irish specimen may represent the last trace of the genus in time. The five-lobed form (Pl. XI, fig. 1) is closely allied to *D. Smithi* Berry. The chief obvious difference is the smaller outer leaflets of the Irish specimen. Berry shows a craspedodrome venation in his restoration, but in his description says it may be camptodrome. Our five-lobed specimen is camptodrome, and is more comparable to the small specimen of *D. insignis* H. and von M. (*op. cit.*). It is unfortunate that *Dewalquea* is known by its foliage only (in many cases fragmentary), and

that identifications have been hitherto, of necessity, based on the macroscopic characters—on the shape, mode of segmentation, and type of venation; with the exception of an observation by Saporta and Marion, nothing hitherto has been revealed of the character of the epidermis. We propose to review the affinities suggested by previous observers in the light of our observations.

Helleborus Affinities.

Saporta and Marion base their rejection of Debey's reference of *Dewalquea* to *Araliophyllum*, and their own reference of it to the Helleboreae, mainly on the peculiar mode of segmentation of the leaf indicated by the term pedalo-digitate. The *Dewalquea* likeness is best indicated in *Helleborus foetidus*, as monographed by V. Schiffner (7). Its leaf is always distinctly pedately divided, and consists of 7–10 small, lanceolate, finely sharp-toothed leaflets. We have failed to note the agreement of the venation of *Dewalquea* with that of *Hellebore*, observed by Saporta and Marion, who were not so fortunate as ourselves in the state of preservation of their specimens, judging from the remark of Hosius and von Marck that the Westphalian material showed poorly preserved secondary veins. We give actual photographic illustrations of the magnified venation of *D. fraxinifolia* (Pl. XII, fig. 3). The secondary veins in *Hellebore* arise at a very acute angle from the midrib, send off branches right and left, and end like their outer branches in the teeth of the leaflet. Each secondary vein is craspedodrome. In *Dewalquea* the secondary veins come off at an angle of 60°–70°, and on nearing the margin bifurcate to join by their forks with adjoining secondaries, which then form a marginal network. They are thus camptodrome. A detailed comparison of the venation does not support the Hellebore affinities of *Dewalquea*. Saporta and Marion describe the epidermis of *Dewalquea* as formed of rounded polygonal cells, with probably sinuous walls like those in *Helleborus*, and, we may add, in many other genera.

Nestler gives a fully illustrated account of the structure of *Helleborus*. Stomata, $45 \times 33\mu$, occur scattered on the under epidermis only. The lateral walls of the lower epidermis cells are sinuous. Unicellular hairs occur, as in Ranunculaceae generally. The upper epidermis shows marked cuticular striation. Peltate hairs are unknown in *Hellebore* or any other Ranunculaceus plant. The geographical distribution is also of interest. The Lower Danube is the "Eldorado" of *Helleborus*, which is exclusively Old World, while *Dewalquea* is represented by many species in the New World, as well as by several in Europe. It would, however, be dangerous to support conclusions of affinities on present-day distribution, there being many cases in which fossil fruits prove the former wider occurrence of a genus or family. The

Ranunculaceae, consisting almost entirely of herbaceous plants, would not lend themselves to fossilization, and their past history is almost a blank in the rocks, though, as members of the *Polycarpieae*, they must have been one of the earliest families of the Dicotyledons to appear. Hellebore, with its coriaceous leaves in some species, would be the one most likely to be found in the fossil state. It would be distinctly satisfying if *Dewalquea* could be accepted as the ancestral form of the family. Its peltate scales, combined with other features, militate, however, against this view.

The Araceae have been suggested as a possible line of affinity with *Dewalquea*. This is admittedly one of the most primitive families of the Monocotyledons, and in, *e.g.* Anthurium, there are several species with pedalo-digitate leaves. Their venation differs, especially in the possession of a marginal vein not found in *Dewalquea*. Their epidermis and stomata also differ. Peltate scales are said to occur, but they are simply saucer-like depressions, in which the secretion of the glandular epidermal cells collects.

A third line of affinity is that indicated by Debey's name of *Araliophyllum*. The *Araliaceae* were rejected by Saporta and Marion on the expert advice of Decaisne that leaves showing such segmentation were not then (as they are now) known in the group. Schimper, as already mentioned, accepted the generic name, and described the fossils as Araliaceous. Peltate hairs occur in *Hedera helix* and in *Oreopanax*, but they are stellate, and do not suggest the disc-like scale-hairs of *Dewalquea*.

P. Principi (8), in his recently published work on the fossil Dicotyledons of the Italian Oligocene, records the Belgian species, *Dewalquea gelindenensis*, and a new species, *D. grandifolia*. He follows Schimper and Zeiller (9) in referring the genus to the *Araliaceae*. *D. grandifolia* shows 5–7 leaflets, each on its own stalk, *i.e.* a compound leaf with 5–7 pinnately arranged terminal leaflets.

The Washing Bay flora is an early one from the Dicotyledonous point of view, and one would hardly expect to find highly specialized families such as the Oleaceae to be well represented in it. Thus in *Fraxinus excelsior* the corolla has passed through the stage of gamopetaly to suppression. *Fraxinus* first appeared in the Arctic regions, and gradually spread southwards in the Old and New Worlds. Heer (10) records *F. praecox* from the Upper Cretaceous beds of Patoot in Greenland; and Lesquereux (11) describes *F. cocenica* from the Eocene of Golden, Colorado; while Ettingshausen and Gardner (12) list *F. jovis* and *F. prae-savinensis* from Alum Bay. The seventeen European species recorded are nearly all referred to the Miocene. One of our specimens (Pl. XI, fig. 6), found at 909 feet, had every appearance of being the distal end of an Ash leaf, such as *Fraxinus pennsylvatica* var. *lanceolata*.

This identification was supported by comparison of the restored epidermis with that of Ash. The subsequent discovery of the quinately divided leaf of *Dewalquea* at 903 feet, with typical epidermal structure, seemed to indicate the necessity of a revision of the first view. In both *Dewalquea* and *Fraxinus* the venation, epidermis, stomata, and peltate scales (glands) all agree sufficiently to allow approximation; and we are of opinion that *Dewalquea* is more naturally associated with the *Oleaceae* than with the *Ranunculaceae*. There is, however, another line of affinity which appeals more to us.

Pl. XI, fig. 9, shows a well-preserved fossil leaf or leaflet, 2 × 4 cm., approximately, coriaceous, broadly oval-lanceolate, margin entire below, but sinuous-dentate in its upper two-thirds, midrib pronounced, thinning out apically; secondary veins fairly numerous but delicate, sub-opposite; angle of divergence, 70°–75°; adjoining secondary veins united towards the leaf edge by loops or their own forkings, and forming a marginal network, from which veins pass into the teeth; the whole system camptodrome. There are no pronounced cross-anastomoses, but there is a fairly well-developed vascular network forming polygonal areas between the secondaries. Shortened secondary veins occur. Externally this leaf shows great resemblance to *Ilex celastrina* Sap. (13), from the Upper Oligocene of Saint Jean de Garquier and Armissan in the south-east of France. As the name suggests, Saporta saw affinity in his specimen to *Celastrus* also, and admits, in naming it, that it is fairly remote in its characters from the *Ilex* of to-day.

If we were confined to a comparison of the external characters only, we should feel compelled to name our specimen *Ilex celastrina*. Restoration of the leaf tissue, however, alters our attitude. Markedly wavy walls are not found in *Ilex* epidermis, nor are peltate scales found in any of the *Aquifoliaceae*, according to Solereder (14). Of the many other possible connexions, the one combining most of the external and anatomical features is the genus *Carya*, *e.g.*, the modern *Carya laciniosa*, in which, however, tufts of hair, not known in our fossil, occur. Our specimen shows, however, such general agreement with *Dewalquea* in its external features and minute structure that we feel compelled to refer it to this genus and not to *Carya*, and to name it *Dewalquea denticulata*. We are of opinion that the leaf fragment named by Heer, *Pterocarya denticulata* ? (15) (*Juglans denticulata* O. Weber) from Bovey Tracey (*op. cit.*, Pl. LXX, fig. 5) is near to, if not identical with, *D. denticulata*; and that the *Carya bilinica* Ettings (16) is also probably nearly allied to it, though differing in form. A re-examination of the collections of fossils in our museums, after restoration by maceration, would reveal many hidden affinities.

Dewalquea shows certain Juglandaceous characteristics not to be overlooked in seeking to ascertain its systematic position. Principi's *D. grandifolia* shows a pinnate leaf of 5–7 leaflets derivable from the types illustrated in the earlier works quoted. The transition from the pedalo-digitate to the impari-pinnate leaf is not difficult to follow. In the seedling of *Pterocarya fraxinifolia* Spach., the two cotyledons are deeply four or five-lobed, and may be described as pedalo-digitate. Such a form of seed-leaf makes it unnecessary to look to the *Hellebore* for an explanation of *Dewalquea's* leaf. Examination of the adult pinnate leaf of *Pterocarya* (and of other genera of the Juglandaceae) shows the presence of peltate scales or glands which bear a striking resemblance to those of *Dewalquea*. In *Engelhardtia* the likeness is such that (Pl. XII, fig. 12) one might easily be mistaken for the other.

The epidermal cells show similar sinuous lateral walls, cuticular surface striae, and similar stomata. There is the same difference in the edge of the leaf as in *Dewalquea*. The edge may be entire or serrate in both genera—in different species in Juglans—but, according to Berry, possibly in the same species (or even plant) in *Dewalquea*. This difference of the leaf-margin is accompanied by a slight difference of venation, which is, generally speaking, camptodrome in Juglans. In this genus the cross-anastomoses connecting the secondary veins run straight and parallel to one another in most cases; but in *Engelhardtia* they are jointed and branched and irregular, as in *Dewalquea*. The secondary veins bifurcate and join together, giving a marginal network much as in *Dewalquea*. The *Juglandaceae* are a primitive group allied to the Amentaceae and Myricaceae. Though *Juglans* is now confined, in Europe, to the south-east corner, it was widely distributed throughout the continent in Tertiary times, having travelled southwards from the Arctic regions. Until fruits are found the question must remain open; but one may provisionally regard *Dewalquea* as an ancestral Walnut.

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EXPLANATION OF PLATES.

PLATE XI.

Figs.

1, 2, 3. *D. hibernica*, sp. n.

1. More or less complete leaf, showing five leaflets.

4–11. *D. fraxinifolia*, sp. n., showing the three leaflets of the leaf in varying degrees of preservation.

8, 9. The two impressions of the same leaflet. (× 2).

12–14. *D. denticulata*, sp. n.

13, 14. Natural size. Fig. 12 (× $\frac{3}{2}$).

PLATE XII.

1, 2. *D. hibernica*, showing the peltate scales. (× 2).

3. *D. fraxinifolia*, venation in detail. (× $7\frac{1}{2}$.)

4. *D. denticulata*, venation. (× 3.)

5, 6. Upper epidermis of leaf of *Dewalquea*, sinuous lateral walls.

7–10. Under epidemis of same, showing stomata and bases of peltate scales. (7–8 (× 80), 9–10 (× 360.))

11. Peltate scale of *Dewalquea*. (× 300.)

12. Peltate scale of *Engelhardtia spicata*. (× 300.)

XXVII.

A SIMPLE FORM OF APPARATUS FOR OBSERVING THE RATE OF REACTION BETWEEN GASES AND LIQUIDS, AND ITS USE IN DETERMINING THE RATE OF SOLUTION OF OXYGEN BY WATER UNDER DIFFERENT CONDITIONS OF MIXING.

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I.—Introduction.

The apparatus described in this paper was primarily devised as an alternative method of carrying out the "Five Days' Dissolved Oxygen Absorption Test," and is based on a principle previously utilized by Professor Adeney for the same purpose.[1]

In the course of the work, however, it became apparent that the principle was capable of wider application, and the apparatus was finally designed with a view to its possible use for the study of gas-liquid systems in general.

The effect of different rates of stirring on the rate of solution of oxygen in water has been determined by means of the apparatus, and the results of the experiments are given in this communication, as they have a direct bearing on some previously published work.[2]

II.—The Principle on which the Apparatus is Based.

The principle utilized in the apparatus depends on the changes in pressure which occur when a liquid is placed in contact with a closed volume of a gas which it is capable of absorbing, and the action of the apparatus will be understood by reference to fig. 1.

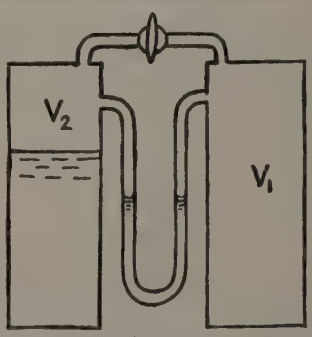

Fig. 1.

In the system shown in the diagram there is a volume of gas V_2 connected through a manometer with a volume of gas V_1, there being sufficient liquid in V_1 to ensure saturation of the gas with vapour, and the liquid under test

[1] Fifth Report, Royal Commission on Sewage Disposal. Appendix vi, p. 438.
[2] Adeney and Becker: Scientific Proc., R.D.S., 1919, xv, p. 609.

is in contact with the gas in V_2. When the tap is closed, any absorption of gas by the liquid from V_2 results in a decrease in pressure, which is indicated on the manometer, and from the manometer reading the volume of gas absorbed can be calculated. With such an arrangement it is possible to vary the sensitivity of the manometer considerably. The smaller the volume V_2 becomes in comparison with V_1, the greater the movement of the manometer (within limits) for a given absorption of gas by the liquid. Further, when the tap connecting V_2 and V_1 is opened, the manometer returns to zero, and the difference in pressure previously existing in V_2 is distributed between the combined volume, thus making it a much smaller fraction of the whole. With such an arrangement it becomes possible to reset the manometer to zero several times during the course of an experiment, without allowing the pressure in V_2 to fall to such a value as would seriously affect the solubility of the gas. The tap also affords an easy method of replenishing the supply of one of the constituent gases of a mixture contained in V_2. Thus, if V_2 contains atmospheric air in contact with a liquid absorbing oxygen, and V_1 contains pure oxygen, then, after a given absorption, the opening of tap resets the manometer, and also replaces the oxygen absorbed to an extent which will depend on the ratio $\frac{V_2}{V_1}$.

The conditions at the start of an experiment are such that the pressures in V_1 and V_2 are equal to each other and to the atmospheric pressure P mm.

Now, suppose an absorption of Q c.c. takes place in V_2, and that the resulting manometer reading is p mm., then $(V_2 - Q)$ c.c. at P are occupying $(V_2 - v_1)$ at P_x, where v_1 = the volume of liquid which has risen above the zero point in the manometer, and V_1 c.c. at P are occupying $(V_1 + v_1)$ c.c. at P_y.

Now, since $$P_y = P_x + p,$$

$$\therefore \quad \frac{PV_1}{V_1 + v_1} = \frac{P(V_2 - Q)}{V_2 - v_1} + p,$$

which gives $$Q = v_1\frac{(V_2 + V_1)}{V_1 + v_1} + \frac{p}{P}(V_2 - v_1).$$

If the two vessels are now connected by opening the tap, P_y becomes equal to P_x, and $p = 0$.

There is then $V_1 + (V_2 - Q)$ c.c. at P occupying a volume $V_1 + V_2$ at P_z.

Hence $$P_z = \frac{P(V_1 + V_2 - Q)}{V_1 + V_2}$$

$$= P\left(1 - \frac{Q}{V_1 + V_2}\right).$$

Hence the pressure in the air spaces after resetting the manometer will be less than that existing at the start by a quantity dependent on the ratio of the volume of gas absorbed to the combined volume of the two air spaces. By making the latter large this quantity can be made very small at will.

III.—Description of Apparatus.

The apparatus which was devised on this principle is shown diagrammatically in fig. 2.

It consists of two cylindrical glass vessels about 30 mm. in diameter, which are connected to two branches of a three-way tap. The lower vessel is of such a size as to contain a suitable volume (say 100 c.c.) of the liquid to be tested, and still leave room for an air space of about 50 c.c.; the upper vessel has also a capacity of about 50 c.c. The three-way tap allows of the two air spaces being connected through the manometer, or directly, according to its position. Hence, when an absorption has taken place, the manometer can be reset to zero by suitably turning the tap.

The whole apparatus, including the manometer, is enclosed in a cylindrical water-jacket, through which water is circulated from a thermostat. The handle of the three-way tap projects through a hole blown in this water-jacket, the joint being kept water-tight by means of a rubber diaphragm. The water-jacket is closed at each end by flanges, which may be made of brass, tin, or ebonite, according to the purpose for which the apparatus is to be used.

The stirrer passes through a long sleeve in the lower flange, and is provided with two conical surfaces, one of which can be

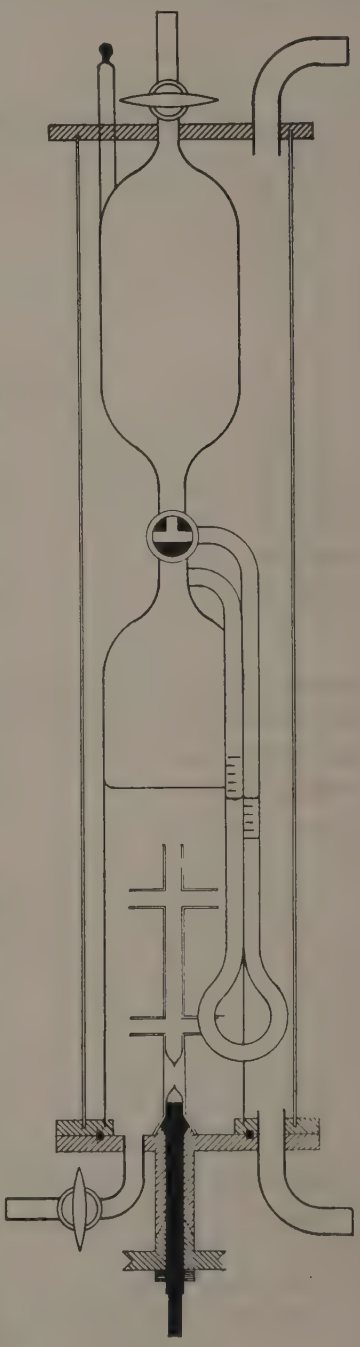

Fig. 2.

adjusted by means of a screw, so that the whole is water-tight. In addition, the glass part of the stirrer is expanded into a cone at the lower end, which is ground to fit a corresponding cone on the bearing, so that the metallic parts of the stirrer do not come into contact with the liquid at any point.

The glass part of the stirrer is so designed that, when rotated at a high speed, it causes a stream of fine bubbles of the gas to circulate through the liquid, thus ensuring equilibrium between the liquid and the gas.

The manometer is provided with a scale of millimeters etched on the glass.

IV.—Calibration of the Apparatus.

In order to check the formula derived for the calculation of the volume of gas absorbed, use was made of ferrous hydrate as an absorbent for oxygen. The following experiments were made:—

The apparatus was filled with 110 c.c. of distilled water which had been previously saturated with air at 20° C. by bubbling air through it for some hours, and the water circulation from the thermostat through the water-jacket started. When everything was in equilibrium, about 25 c.c. of the water was withdrawn, and in place of it was added exactly 10 c.c. of a solution of ferrous sulphate containing 8·2 grams per litre, followed by 10 c.c. of a 10 per cent. solution of sodium carbonate, the whole being carefully washed into the apparatus. The barometer was then read, and the taps of the apparatus having been suitably adjusted, the stirrer was started, and the manometer watched until the reading became constant. The maximum reading was then used to calculate the volume of oxygen absorbed by the ferrous hydrate.

Experiment A.—Temperature, 20·0° C.; barometer, 768·1 mm.

Maximum reading of manometer,	. 114·0	divisions.
Second reading after resetting to zero,	. 5·5	„
114 divisions at 768·1 mm. correspond to	1·525	c.c.
5·5 „ „ „	·073	„
	Total, 1·598	

Total volume absorbed, calculated for N.T.P. = 1·504 c.c.

Experiment B.—Temperature, 20·0° C.; barometer, 769.9 mm.

Maximum reading of manometer, 118 divisions.

118 divisions at 769·9 mm. correspond to 1·610 c.c., which at N.T.P. reduces to 1·520 c.c.

The mean of the two experiments gives 1·512 c.c. absorbed.

Since the partial pressure of the oxygen in the air in the vessel was

reduced from $\frac{10{\cdot}5}{50}$ to $\frac{9{\cdot}0}{50}$, a correction for this must be applied. The pressure in the vessel before the experiments was 768·1 mm., and at the end was 758·0 mm.

Taking the composition of atmospheric air to be approximately: nitrogen, 79 per cent., oxygen, 21 per cent., and the coefficient of absorption of oxygen as 0·0310 at 20° C., we can calculate the amounts of oxygen in solution at the beginning and at the end of the experiments.

The pressure of aqueous vapour at 20·0° C. is 17·5 mm.

The volume of oxygen in solution at the start is—

$$V_0 = \cdot0310 \times 110 \times \frac{10{\cdot}5}{50} \times \frac{750{\cdot}6}{760} = \cdot706 \text{ c.c.}$$

The volume in solution at the end is—

$$V_1 = \cdot0310 \times 110 \times \frac{9}{50} \times \frac{740{\cdot}5}{760} = \cdot598 \text{ c.c.}$$

Hence the difference due to change in the saturation value is ·108 c.c., and this, when added to the volume indicated by the manometer reading, gives a total of 1·62 c.c. as the actual absorption.

The 10 c.c. of ferrous sulphate used should have absorbed 1·64 c.c. oxygen according to its titre by potassium permanganate, hence the two values agree within $1\frac{1}{4}$ per cent.

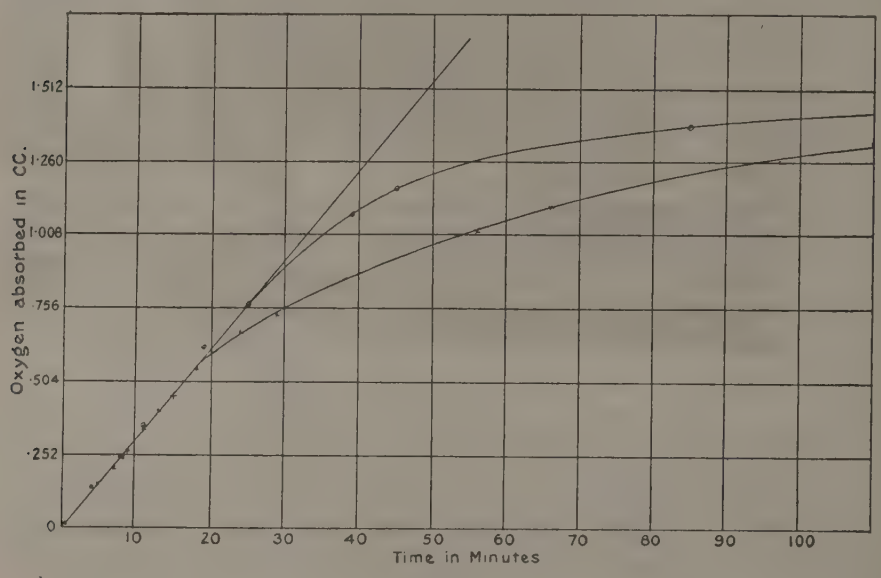

Fig. 3.

The graph, fig. 3, shows the course of the absorption. During the first part of the absorption the water is completely de-aerated by the excess

of ferrous hydrate, and, consequently, the oxygen is absorbed at a constant rate, as shown by the fact that the graph at this portion is practically a straight line. In the second stage, when all the ferrous hydrate has been oxidized, the absorption falls off gradually, so that the graph becomes a logarithmic curve. During this stage the water becomes completely re-aerated. In the figure, the second graph shows a more gradual approach to saturation than the first; this is due to the fact that during this experiment the speed of the motor driving the stirrer varied suddenly owing to variation in the voltage of the supply. This observation indicated the advisability of determining the time necessary to attain equilibrium under certain conditions. As this was intimately connected with some work which had been done previously on the rate of solution of gases by water, it was considered worth while to examine it more fully.

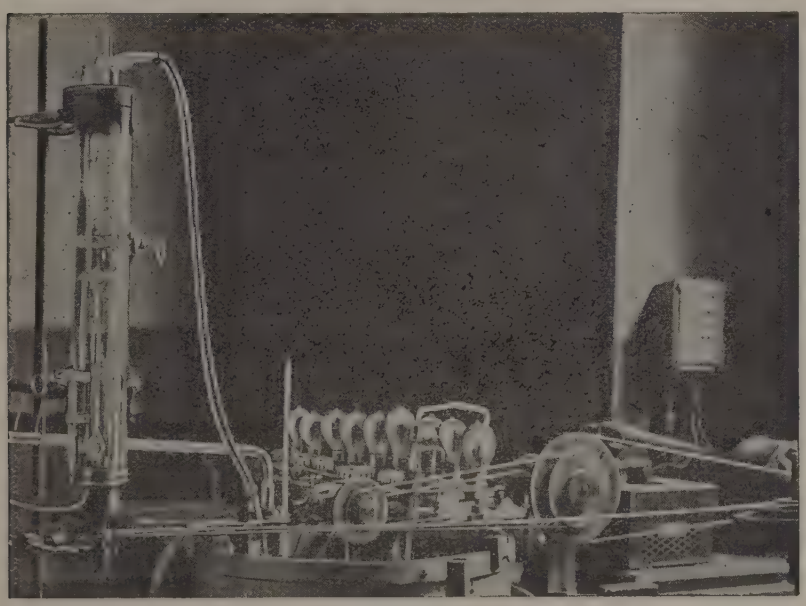

Fig. 4.

V.—Experiments on the Effect of Stirring on the Rate of Solution of Oxygen in Water.

The method consisted in introducing into the apparatus known amounts of a solution of ferrous sulphate and precipitating the hydrate by means of a solution of caustic potash; the stirrer was then driven at certain definite speeds by means of a small alternating-current motor (which could be relied upon not to vary in speed to any large extent), and the rate at which the oxygen was absorbed noted by observing the manometer.

The complete apparatus used for these experiments is shown in the photograph (fig. 4). The motor at the right of the picture drives the small circulating pump (which is immersed in the water in the thermostat), and also a stirrer in the thermostat. The water is pumped along the horizontal glass tube to the left, and into the water-jacket of the apparatus already described, from which it returns to the thermostat by the rubber tube from the top.

To the extreme right will be seen one of a series of horizontal pulleys which were connected to the small alternating current motor in order to give the desired variation in speed of stirring. This pulley is connected to the stirrer of the apparatus by the long belt appearing in the foreground, thus imparting motion to the stirrer at a rate which could be determined by the ratio of the various pulleys. The water circulation was continued, and the stirrer run at a constant speed during the course of each experiment.

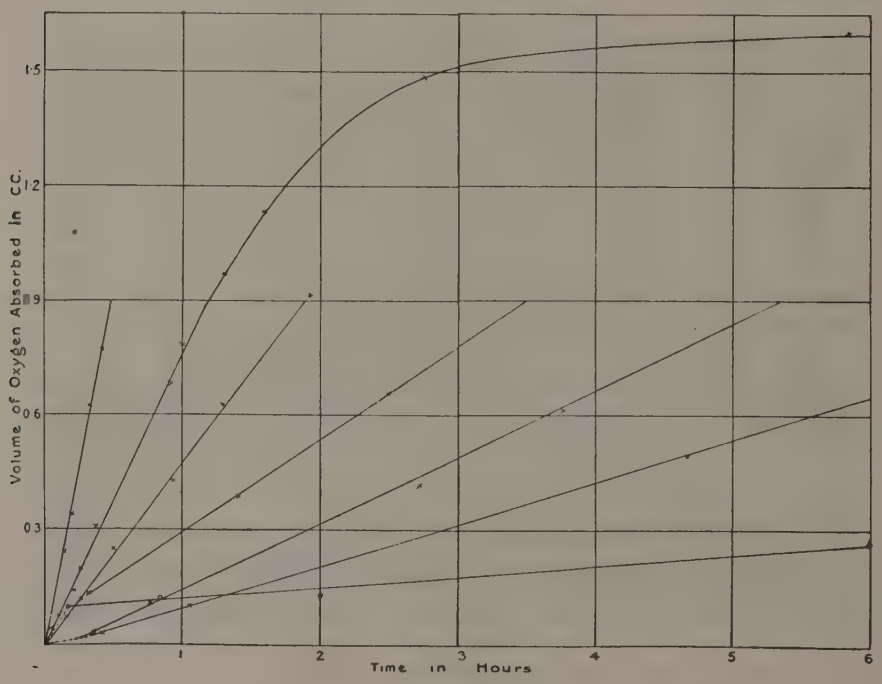

Fig. 5.

The lower speeds of revolution were counted directly, using a stop-watch to check the time, and for the higher speeds the rate of one of the slower moving pulleys was found and that of the stirrer by calculation.

Five experiments were made with different rates of stirring, and one experiment was made to compare the rate at which quiescent water absorbs oxygen with the rates at which the thoroughly stirred water absorbs it. The results of these experiments are shown in fig. 5.

The rate of stirring in these experiments varied from zero to about 1,000 revolutions per minute. The lower rates up to about 140 revolutions per minute did not appreciably distort the surface of the water, but above this speed the surface varied in shape and area with each variation in the speed of the stirrer. The shapes assumed by the water surface are shown in fig. 6; and it will be seen that they range from the nearly flat surface of still water to the point at which the air is drawn down into the water in small bubbles. At this point the surface area becomes uncertain, so that no conclusions can be drawn from experiments at higher speeds. In the other cases the surface area was taken to be approximately equal to that of a cone with the vertical axis equal in depth to that attained by the lowest point of the water surface.

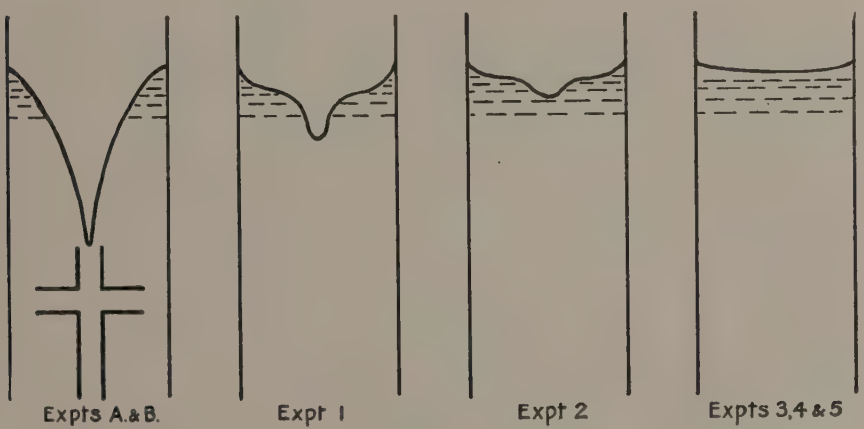

Fig. 6.

The progress of the absorption followed a linear law, as will be seen from the graph, fig. 5, and this shows that the ferrous hydrate de-oxygenated the water completely almost at once, so that the rate of solution of the oxygen remained constant until all the hydrate was oxidized.

The variation in the value of the rate of solution with stirring is shown in the table and in fig. 7. On the graph the lower line shows the rate of solution under the conditions of the experiment plotted against rate of stirring, and the points lie approximately on a straight line. Hence under the conditions of these experiments the rate of solution varies directly as the rate of stirring.

Values of Rate of Solution for different Rates of Stirring.

Experiment.	Speed of Stirrer, r. p. m.	Estimated Areas of Surface, sq. cm.	Rate of Solution in c.c. per min.	Rate of Solution per unit area. $S = \frac{a}{A}$.
A and B.	1000	19·0	·030	·0016
1	590	11·1	·014	·0013
2	340	8·8	·008	·0009
3	140	8·1	·004	·0005
4	80	8·1	·003	·0004
5	60	8·1	·002	·00025
6	0	8·1	·0001	·00001

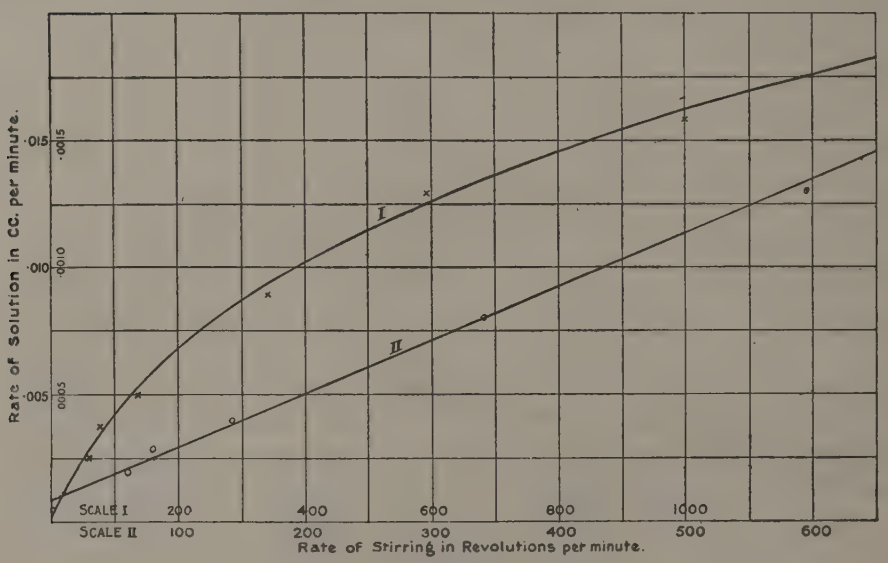

Fig. 7.

When, however, the effect of increased surface area is taken into account, and the rate of solution per unit area plotted against rate of stirring, the result is the upper line in fig. 7. This curve shows the rapid increase in the rate of solution at first, which gradually falls off as the higher values are reached, and tends to reach a maximum.

VI.—COMPARISON OF RESULTS.

The results obtained in Experiment 6 are shown as a graph in fig. 8 in order to afford a comparison between the rate at which the oxygen is absorbed by quiescent water and the rate when the water is stirred. The water was at first stirred for two minutes in order to mix the ferrous hydrate with the liquid, and thus reduce the oxygen content to zero. During this period the rate of absorption was of the same order as obtained in the other experiments. The stirring was then stopped, and the rate fell off slowly as the liquid came to rest until it reached a value which remained nearly constant for three days. On the third day this suddenly changed for a higher value, which remained constant until the sixth day, by which time only about half the saturation value had been reached. The liquid was then stirred again, and the remainder of the absorption was completed in about five hours. Hence a process of absorption which may take many days to complete when the water is quiescent takes place in as many hours with moderate stirring.

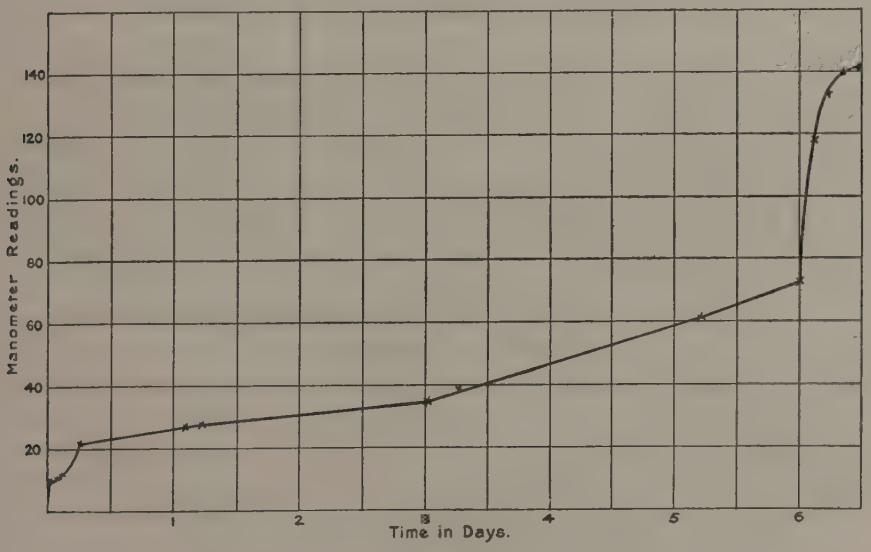

Fig. 8.

The sudden change in the rate of solution of oxygen by the quiescent water indicated above is characteristic of the process under these conditions, for the rate of solution of gases by water is then liable to sudden and unaccountable variations within narrow limits.

The greatest value for the rate of solution per unit area given in the table represents the maximum rate attainable under the conditions of these

experiments, without allowing the surface exposed to become indefinite : hence it is of interest to compare this with the rate of solution as determined in previous experiments.[1]

The rate of solution of oxygen into air-free water has been found by a totally different method to be ·0161 c.c. per minute per square centimetre of area exposed. Hence for the oxygen in the atmosphere the rate should be $\cdot0161 \times \frac{21}{100} = \cdot0034$ c.c. per minute under similar conditions, since the rate of solution has been shown to be proportional to the partial pressure.

This value is more than twice as great as the maximum value attained in these experiments (·0016), showing that the rate of mixing that was reached under these circumstances was not so rapid as that obtaining in the experiments referred to. This was to be expected, since in those experiments the water was exposed to the oxygen in very thin layers, and very perfectly mixed immediately afterwards. However, the fact that the two values come so near each other shows that with more perfect stirring arrangements it might be possible to approximate very closely to the maximum rate of solution.

These experiments therefore afford a connecting link between the conditions obtaining in the work referred to and those obtaining in nature. They also emphasize the important part played by mixing of the water in determining the rate of solution. It will be seen on reference to the table that very gentle stirring of the under layers of the water increases the rate of solution as much as twenty-fold as compared with stationary water. This bears out the view put forward previously,[2] that the rate of solution of air by water under ordinary conditions is largely determined by the rate of mixing. Experiments are being continued with this apparatus; and it is hoped to publish further results in the future.

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[1] Adeney and Becker: Scientific Proc. R.D.S., xv, p. 625. 1919.
[2] Adeney and Becker: Scientific Proc. R.D.S., xvi, p. 143. 1920.

XXVIII.

THE OCCURRENCE OF A SEQUOIA AT WASHING BAY.

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AND
JANE G. GILMORE, B.Sc.

[Plates XIII, XIV.]

Read June 28. Published August 29, 1921.

In the course of examination of the Washing Bay core we have met with not only isolated seeds and pollen-grains of the genus *Sequoia*, the only Conifer found in it, but fortunately foliage shoots and cone-bearing twigs also, enabling us to identify the fossil.

Sequoia (or Wellingtonia) has a very limited present-day geographical range, being confined to the west Pacific coast of North California (and Oregon). One species, *S. sempervirens* (Sargent) (1), the Redwood, grows on sandstone to the height of 400 feet and a diameter of 28 feet, exposed to the warm Pacific winds and fogs, mainly in a mountain forest belt along the coast of California; it ascends to 3,000 feet, and rarely occurs inland more than 20 miles. *Sequoia gigantea* or *Sequoia Wellingtonia* (1) (Sargent sp.), the Mammoth tree, the other living species, grows between 36°–39° N., on the western slopes of the Sierra Nevada, up to elevations of 8,000 feet, lives to 4,000 years of age, reaches a height of 320 feet or more, and a diameter of 35 feet.

Though now recognized as one of the wonders of nature, the first-named of these giants of the forest was not discovered until 1847, a date it is well to keep in mind in criticizing the Conifer identifications of the earlier palaeobotanists (e.g., of the Mull plants). It is generally agreed that *Sequoia*, the only member of the family Sequoiineae, is a very ancient genus, and represents one of the earliest families of Conifers. It has been traced, at any rate, to the earliest Cretaceous beds, increasing in frequency and variety of form into the Miocene, in which it is represented by many species. It was one of the many circumpolar or Arctic genera which radiated southwards during the Cretaceous and early Tertiary epochs. Like many other genera now confined

to North America or to East Asia, it flourished at one time in Europe, and fell before a lowered temperature and other adverse conditions. C. and E. M. Reid (2) describe and illustrate a cone from the Pliocene beds on the Dutch-German border as probably the last trace of *Sequoia* in Europe. E. W. Berry (3) gives a useful map (fig. 1) showing the almost world-wide distribution of *Sequoia* during the Tertiary epoch, in striking contrast to its present restricted area. Its occurrence in New Zealand, South-East Australia, and South America, the only localities recorded by him in the Southern Hemisphere, is worthy of note, and seems in need of critical confirmation. West and Central Europe, North-East Asia, North America, and the Arctic regions were its chief centres.

Sketch Map showing the location of Caenozoic records of *Sequoia*.
After Berry, from "The Plant World."

It will be well to state here the distinguishing characters of the foliage of the living species of *Sequoia* for comparison with fossil forms. In both species the leaves are mostly spirally arranged, and more or less clearly decurrent. In *S. sempervirens* the base of the leaf is so twisted that the leaves appear distichously arranged. They are yew-like, linear, and flattened, with a single vein as midrib. The apex may be acute or obtuse. In *S. gigantea* the spiral arrangement is undisturbed and obvious, the leaves narrow and subulate, roughly three- or four-sided (rhomboidal), with one vein. They are more or less adnate or adpressed in their lower part, spreading above. Their ridged bases are so decurrent and close together as to cover the whole surface of the stem, thus leaving no part of the stem surface proper exposed. Further, in both species there are small ovate-triangular, squamiform, keeled, closely adpressed, spirally arranged leaves. Thus both species are dimorphic. The squamiform leaves occur on the cone-bearing shoots in both species, and at intervals on the foliage shoots of *S. gigantea*. They occur in *S. sempervirens* also at the tips of the foliage shoots, making its buds "scaly" in contrast to

the "naked" buds of *S. gigantea.* They also occur at the bases of the foliage shoots of *S. sempervirens,* being in reality the persistent bud-scales through which the foliage shoot has grown and elongated. S. Gardner (4) notes the interesting fact that when introduced into a warmer climate, such as that of Madeira, *S. sempervirens* develops more of these leaves, an indication apparently of more vigorous growth in a warmer climate, with consequent formation of bigger buds. This may indicate that adpressed foliage is more adapted than the spreading foliage to a warmer climate. A reduction of transpiration and an exposure of one side only to sunlight, if bright, are obvious advantages of adpression. One would expect such foliage in ancestral *Sequoias* growing in the tropical or subtropical conditions of the Cretaceous or early Tertiary. It is the prevailing type in our *Sequoia* and in that of Bovey Tracey (5). We hope to prove that the *Sequoia* found in the two localities is identical, and the beds containing it contemporaneous, viz., *Sequoia Couttsiae* Heer in the Upper Oligocene.

As already mentioned and as our illustrations (Pl. XIII, figs. 1–9) show, *S. Couttsiae* Heer possesses in the main an adpressed foliage. The leaves are semi-ovate or triangular, imbricate, decurrent, more or less falcate, with acute apex, and are spirally arranged. Each leaf is keeled or ribbed in correspondence with its solitary vascular bundle. One frequently finds at the tip of the leaf a sharp-pointed brittle cap of amber (Pl. XIII, fig. 10), which has evidently oozed out from the single resin-passage known to occur in the leaves of recent *Sequoias.* Under the dissecting microscope one can detach the amber tip and leave the leaf apex blunter in consequence.

The leaves are readily restored. Stomata (Pl. XIII, figs. 11–12) occur on both surfaces, and on the lower side form two bands, one on either side of the midrib. With a view to testing the taxonomic value of the arrangement and character of the stomata, we made a series of preparations of the leaf of living *Sequoia* and other Conifers.

C. and E. M. Reid (6) were able by restoration of the epidermis of the Bovey Tracey material to show that Heer's species was rightly named; that it was a *Sequoia,* and not, as S. Gardner stated, an *Athrotaxis.* It needs little knowledge of the Conifers to make one realize the helplessness of positive identification based on the external characters only of the foliage, owing to its pronounced heteromorphism. With differences of form supported by difference of microscopic characters there is more hope of success. A reliable way of distinguishing *Sequoia gigantea* from *Cryptomeria japonica* and *S. sempervirens,* and *S. Langsdorfii* from *Taxodium distichum* microscopically would be distinctly helpful. Bertrand (7) could find no difference in the epidermis of *Sequoia* and *Cryptomeria* in the distribution or arrangement of

the stomata or in the structure of the epidermis. We find, however, a marked difference in the size of the stomata. Those of *Sequoia* are 56–64μ long; those of *Cryptomeria* only 40–46μ in our material. If this difference held good in general, it would be a useful means of discrimination. The following table gives the results of measurement of the length of the stomata:—

	μ
Sequoia gigantea, ...	56–64
„ sempervirens, ...	56–64
„ Couttsiae, ...	52–66
„ "du Noyeri,"	48–60
(Cryptomerites du Noyeri Seward)	
Taxodium distichum, ...	46–56
* „ mucronatum, ...	46–56
Cryptomeria japonica, ...	36–46
*Glyptostrobus heterophyllus (South China), .	40–46
* „ „ (Hong Kong), .	54–62
*Taiwania cryptomerioides, ...	56–66
Athrotaxis laxifolia, ...	36–44

It will be seen that the fossils referred to *Sequoia* agree with the living species of the genus, their smallest stomata being larger than the largest ones of *Cryptomeria*.

The *Glyptostrobus* measurements seem to cast doubt on the taxonomic value of the size and arrangement of the stomata. Those in the specimen from South China, showing spreading yew-like foliage, lie parallel to the long axis of the leaf, and are of the size of those of *Cryptomeria* in contrast to those in the Hong Kong specimens, with adpressed foliage, which, though on the whole parallel to the long axis, are less regularly arranged, and of a size comparable to those of *Sequoia*.

While in most of the species listed stomata occur on both upper and under surface of the leaf, in *Athrotaxis laxifolia* they are confined to the upper surface. The stomata on the under side of a leaf generally form two bands or ribbons parallel to the midrib. In the ribbon one may see in many cases distinct rows or files of stomata. When the leaf is decurrent the bands can be traced on to the stem. These "stem" stomatal bands are particularly well marked in *Glyptostrobus*. In *Sequoia* the individual stomata lie with their long axis for the most part parallel to the midrib; in *Cryptomeria* they are more irregularly arranged. Florin, who has investigated the epidermal

* We are indebted to Professor A. Henry for this material.

structure of the leaf of a number of Conifers, citing Mahlert in support, notes that in *S. gigantea* all the stomata lie with their longitudinal axis parallel to the direction of the bundle, while in *S. sempervirens* numerous transitional positions also occur. In our investigation of *Sequoia*, before we had Florin's results, we found that, while the stomata in *S. sempervirens* lie parallel to the midrib in the normal spreading foliage, they are less regularly arranged in the leaves of its fertile shoots, and in the general foliage of *S. gigantea*.

Taxodium distichum shows the stomata in the two bands arranged lengthwise in series, but also transversely in rows. Each stoma, on the whole, lies with its long axis horizontally placed, i.e., at right angles to the direction of the vein. *Taxus baccata* shows stomata in vertical rows parallel to one another, the individual stomata in each vertical row looking like links in a chain, with vertical longitudinal axis. The mode of arrangement of the stomata should prove a valuable diagnostic character in distinguishing between fossil *Taxodium* and *Sequoia*, e.g., *T. distichum miocenicum* and *S. Langsdorfii*, in which we have so far failed in our attempts at restoration by maceration.

While the adpressed squamiform leaf, 2–4 mm. long, is the prevailing type in *S. Couttsiae*, narrow, acicular, or subulate, sometimes markedly divaricate leaves, 4 mm. long, also occur (Pl. XIII, figs. 6–9). We have many twigs bearing these leaves only, and were struck by their similarity to the specimens from the Interbasaltic beds of Co. Antrim, named by Baily *S. du Noyeri* (8). One specimen (Pl. XIV, fig. 1) from the Grainger collection in the Belfast Museum shows both types on the same shoot, and the resemblance to the fertile shoot of *S. gigantea* is marked. The type specimen of *S. du Noyeri* Baily (Pl. XIV, fig. 2) shows impressions only, in the ironstone. As our photograph of the type shows, Baily's drawing (Pl. XIV, fig. 3) makes the leaf much too long. This figure may have led Gardner to conclude that *S. du Noyeri* was really a *Cryptomeria*. We are of opinion that it is a *Sequoia* and, at the most, a form of *S. Couttsiae*.

It is clear from Saporta's illustrated account of *S. Couttsiae* var. *polymorpha*, that a form of *S. Couttsiae* grew in the south-east of France not unlike the *du Noyeri* form of *S. Couttsiae* in north of Ireland, the Baltic region, and Greenland.

If Gardner's drawings of cones of the Glenarm material are correct, then we must admit that *Cryptomeria*, now confined to China and Japan, grew in Co. Antrim in the Tertiary. It is not, however, recorded elsewhere in the fossil state. We have restored the epidermis of the leaf of a Conifer from Glenarm. It has all the characters of a *Sequoia*. In the same slab are winged seeds (Pl. XIV, fig. 13) indistinguishable from those of *S. Couttsiae*,

and unlike the almost wingless seed of *Cryptomeria*, which was evidently not, as Gardner thought, the only Conifer at Glenarm.

Pollen-grains are frequent throughout the part of the core examined. They are spherical, finely punctate, 25–31μ in diameter, and agree with the fresh pollen-grains of *S. gigantea*. More than once bodies like Pl. XIV, fig 4, occur, indicating a pollen mother cell in course of division. They may or may not belong to *Sequoia*. The branching shoot shown in Pl. XIV, fig. 5, is interesting, but, without breaking it up, it is difficult to decide as to the nature of the two swollen terminal buds. They may be scaly foliage buds, male flowers, or even young cones. No signs of pollen-grains were obtained by examination of the restored counterpart. Cones, however, occur, as well as isolated seeds, and we had the good fortune to find one cone split open—borne on a shoot carrying true *S. Couttsiae* leaves (Pl. XIV, figs. 6–7)—in such a way as to show its structure as clearly as if it were a median section of a fresh cone. Several seed-bearing scales are exposed. Seeds (Pl. XIV, figs. 7–10) are observable on the upper surface of each scale, overlapping one another, being inverted or pendulous, 3·5 mm. long, 2·7 mm. broad at the base. Each seed shows a central somewhat curved "nucleus," with two fairly broad lateral wings. The seed is pointed or apiculate at its lower or micropylar end, broader and emarginate at its upper basal attached end. The hilum as a disc-like scar is clearly observable. The seeds are attached at the distal end of the ovuliferous or bract scale. A casual inspection of Sargent's figures of the seed scales in the two living *Sequoia* will suffice to show a marked difference in the arrangement of the seeds in the two. It is worthy of note that *S. Couttsiae* agrees with *S. sempervirens*, and not with *S. gigantea*, in the size and structure of its cone and arrangement of its seeds. The main (adpressed) type of foliage of *S. Couttsiae* is strictly localized in *S. sempervirens*, and only here and there observable in *S. gigantea*; otherwise it is buried in the past. It may be added that the cone of *S. sempervirens* ripens in one season, but, according to Sargent, that of *S. gigantea* ripens in the second season, as in *Pinus* and other Abietineae.

There is a certain amount of lignite in the core, and some of our preparations show typical Conifer tracheides, with a single row of bordered pits (Pl. XIV, fig. 10) on their radial walls, much as in recent *Sequoia* wood. We hope to make a more thorough examination of the lignite later. As *Sequoia* and *Taxodium* are usually associated with lignite deposits, a second boring might reveal larger deposits of lignite, giving a fuel capable of utilization in the baking of the enormous thickness of clay which makes, we understand, a satisfactory, though coarse, kind of pottery.

S. Couttsiae Heer seems to have suffered a good deal at the hands of investigators. Heer's drawings, supplemented by the photographic illustrations of C. and E. M. Reid, leave one in no doubt of the general characters of the species. Heer gives a figure (*op. cit.*, fig. 12) of *S. Couttsiae* showing linear leaves, longer and more divaricate than usual, but he shows in fig. 9 the transition to the normal type. He clearly realized the dimorphism of *S. Couttsiae.* We have before us material from Bovey (Pl. XIV, fig. 11) (Reid Collection, York Museum), Co. Antrim (Grainger Collection, Belfast Museum) (Pl. XIV, fig. 1), Disco (Dublin Museum) (Pl. XIV, fig. 12), as well as Baily's type specimen of *S. du Noyeri* (I. G. Survey) (Pl. XIV, fig. 2). We are of opinion that *S. Couttsiae* Heer was common to Greenland, Ireland, and Devonshire, and that *S. du Noyeri* Baily and *S. Whymperi* Gardner should be treated as synonyms.

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EXPLANATION OF PLATES.

Plate XIII.

Figs.

1–9. Branches of *Sequoia Couttsiae* from Washing Bay.

1–5. Shoots with squamiform foliage.

1–3 are magnified. (× 3.)

6–9. Shoots showing acicular leaves, occasionally divaricating. (× 3.)

10. Resin tips of leaf. (× 80.)

11. Stomata from squamiform leaf of *S. Couttsiae*. (× 240.)

12. Stomata from acicular leaf of *S. Couttsiae*. (× 240.)

Plate XIV.

1. The two types of foliage on the same shoot of *S. Couttsiae*. (Grainger Collection, Belfast Museum.)

2. Type specimen of *S. du Noyeri* Baily. (Irish Geolog. Survey Collections.)

3. Photograph of Baily's restoration of specimen in fig. 2.

4. Pollen mother-cell dividing. *Sequoia?*

5. Branch of *S. Couttsiae* with terminal buds. Male flowers? (× 3.)

6. Cone of *S. Couttsiae*. ($\frac{1}{1}$.)

7. Scale of cone, with overlapping seeds attached. (× 8.)

8. Shoot of *Sequoia Couttsiae*, showing foliage and exposed seeds. (× 3.)

9. Isolated seed of *S. Couttsiae*, showing micropole (m) and hilum (h).

10. Tracheides, showing bordered pits.

11. Foliage of *S. Couttsiae* from Bovey Tracey. (York Museum.) (× 3.)

12. Foliage of *S. Couttsiae* from Disco Islands, Greenland. (Botanical Collections, National Museum, Dublin.) (× 3.)

13. Seed of *S. Couttsiae* from Glenarm. (× 3.)

XXIX.

THE SOURCES OF INFECTION OF POTATO TUBERS WITH THE BLIGHT FUNGUS, *PHYTOPHTHORA INFESTANS*.[1]

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I.—Previous Work on the Manner of Tuber Infection.

In his important paper on the control of potato blight, Jensen[2] distinguishes between two periods during which infection of the tubers occurs. The first is while they are still *in situ* in the soil; and the decay set up by the parasite is generally obvious at digging time, or at the latest by about one week after that operation. The second occurs during lifting, a copious development of Phytophthora rot setting in about one week after the potatoes have been dug.

Jensen, if he was not the first to draw attention to the danger of digging the crop while any green foliage remains on diseased plants, appears to have been the first, at any rate, to emphasize the magnitude of the danger, to give a rational explanation of it, and to suggest a remedy.

According to this author, "si l'on arrache les pommes de terre avant que les fanes soient complètement mortes et pendant que les feuilles portent encore des quantités de spores capable de germer, ces spores vont tomber en quantité sur les tubercules . . . et une semaine après ou un peu plus tard, si la température est basse, l'effet fatal s'en fera sentir." And it is further stated: "si l'on retarde l'arrachage jusqu'à ce que les spores soient mortes, c'est à dire environ deux semaines après le dessechement des fanes, tout danger est evité."

There are quoted in support of this view the results of two experiments

[1] Acknowledgment is made to the Department of Agriculture of the Dominion of Canada for permission to publish in advance the results of experiments carried out in that country.

[2] Jensen, J. L.: "Moyens de combattre et de détruire le Peronospora de la pomme de terre." Mém. Soc. nat. d'Agriculture de France, t. cxxxi. 1887.

in which portions of plots were dug successively on September 7th, 12th, 15th, and October 11th. The following percentages of the crop developed Phytophthora rot:—1st digging, 21·5; 2nd digging, 33·5; 3rd digging, 13·0; and 4th digging, 0 per cent. As to the condition of the foliage during this period, it is stated that a certain amount of foliage was still green and covered with spores when digging was first begun; at the second and third diggings almost all the leaves were withered, but some spores were still present, while at the last date all the leaves and stalks were dried up. Rain which occurred during lifting was held responsible for the large percentage of rot occurring in the second lot of potatoes which were dug on September 12th.

While Jensen had reached the conclusion by experimental methods that soil to which spores had been added remained capable of causing infection for a longer period than the spores themselves continued to be viable while still on the leaves, and that in fact spores which had actually fallen to the ground might prove sources of infection to the tubers during the operation of digging, he over-estimated the importance of infection arising directly from diseased foliage, and under-estimated the part played by contaminated soil. His final conclusion was that the crop was likely to decay in storage if it was dug too soon, "c'est à dire pendant que les spores se trouvaient encore dans les feuilles."

To his belief in this theory is traceable the inconsistency noticeable in the practical directions which he gives for the control of tuber rot after digging. Thus, he found experimentally that only about 1 per cent. of the spores produced on the leaves survived a dry day; and that soil with which spores had been mingled induced rot in potato slices up to five days afterwards, indicating a length of spore life of five days in the soil. In spite of these results it was found necessary in practice to refrain from digging for as long as two weeks after the complete drying of the foliage. Nevertheless, he believed that where it was not possible to delay digging sufficiently long to allow an interval of even five or six days after the removal of the stalks, the danger could be considerably reduced by such precautions as refraining from digging during rain, beginning work at the windward side of the field, digging in the afternoon rather than in the morning, and especially by removing the stalks, even though digging was to follow immediately. An experimental basis for the latter conclusions, which suggest an ephemeral character for the spores of the fungus, and neglect the possibility of infection from contaminated soil, is not given.

Jensen's conclusions as to the danger of digging the crop while the foliage is blighted were tested experimentally in the United States by Jones and

Morse.[1] The results are summarized by Jones, Giddings, and Lutman[2] as follows:—" . . . where the tops are attacked by the late blight the harvesting of the tubers should be delayed until a week or more after the death of the tops." In the results of two experiments quoted 55·3 per cent. and 18·4 per cent. of the potatoes rotted when they were dug early, while the percentages of rot in similar potatoes dug from three to four weeks later were 7·3 and 6·0 respectively. The condition of the foliage as regards blight was not stated.

Jones and his co-workers did not go into the question of the source of tuber infection after the foliage was practically or completely dead, although they seemed to have assumed that such infection was possible. Jensen proved that the spores remained viable for five days in soil, but his work necessitates the assumption that tubers may contract the disease during more than double that period after the foliage is dead. If this actually takes place, it is necessary to assume an unsuspected amount of vitality in the spores of *Phytophthora infestans* or the existence of some hitherto undiscovered phase in the life-history of the fungus.

II.—PHYTOPHTHORA TUBER-ROT IN EASTERN CANADA.

The present author was led to a consideration of the question of the sources of tuber infection by residence for some years in the Maritime Provinces of Canada, where the ravages of blight developing in the tubers after the crop is dug sometimes exceed the damage wrought by the disease on the growing crop. A considerable number of blighted tubers are sometimes found when the crop is lifted, yet at other times such tubers may be almost absent. When, however, the apparently healthy portion of the crop is stored, in many cases an outbreak of Phytophthora rot sets in which may destroy a large proportion of the tubers. In some cases the result is that not the one-twentieth part (or thereabouts) of the normal crop required to supply "seed" for the following year survives. The sale of tubers may be almost entirely held up for a month or two in the autumn in bad years, because buyers are afraid to touch any potatoes, no matter how sound they look. After the latter part of October the danger is held to be over, as the disease will by then have developed far enough to be recognized.

[1] Jones, L. R., and W. J. Morse: "Potato Diseases and their Remedies.—Relation of date of digging to development of rot." Vermont Agr. Experiment Station, Fifteenth Annual Report (1901–2), pp. 219–223, 1902; Sixteenth Annual Report (1902–3), pp. 161–162, 1903; Seventeenth Annual Report (1903–4), pp. 391–395, 1905.

[2] Jones, L. R., N. J. Giddings, and B. F. Lutman: "Investigations of the Potato Fungus, *Phytophthora infestans*." U.S. Dept. of Agriculture, Bureau of Plant Industry, Bull. 245. 1912.

The reason for the development of such a severe attack late in the season seems to be twofold. The climate in late summer and autumn is almost always such that blight is present, and yet in many cases a balance is maintained, so that both plant and parasite go on developing until up to, or nearly up to, digging time. There is frequently no frost in the coastal districts until late October or even early November; and the season is so short (June 1st to October 15th) that the stalks do not die from natural maturity. In the second place, some of the varieties grown there are standard American potatoes, which, as is well known, are on the whole very susceptible to blight, and are not suitable for cool coastal regions. Due to this combination of circumstances, the results about to be described have a significance for portions of Eastern Canada which is not, perhaps, equalled elsewhere; but, as will be shown, the same factors also operate in Ireland to some extent.

The observation was made in 1915, the first season spent in Canada, that a conspicuously small amount of tuber disease followed a most severe blight attack, which completely killed all the foliage early in September. As it turned out, this was the most serious blight epidemic which occurred in the five-year period 1915–1919, yet the amount of tuber rot which followed was far lower than in any of the other years mentioned. The total amount of Phytophthora tuber rot developed by the crop in that season, including that found in storage up to the following April, was only 1·2 per cent., while the corresponding average for the succeeding four years[1] was 26·3 per cent. In none of the latter years was the blight sufficiently severe as a rule to kill the foliage completely before the crop was dug. The attack, therefore, persisted longer, to which fact is generally attributed the greater amount of decay in the tubers, because of their being exposed to infection for a greater length of time.

It is generally agreed that a long period of spore discharge (that is, a moderate and long-continued attack of blight) and severe tuber rot are associated; and the prevalent view is that the latter is a direct consequence of the former. The assumption must then be made that more spores find their way to the soil when the blight never (or certainly not for a long time) develops sufficient intensity to kill the plants, than happens when the blight attack is much more severe but less protracted; or, alternatively, that under the former conditions the spores reach the tubers in greater numbers or under more favourable conditions for infection. These are hypotheses which

[1] The figures for 1919 do not record the amount of tuber rot developed after November, but they include the severe outbreak which generally occurs within the first month after harvesting, subsequently to which little or none develops.

should be susceptible of experimental proof, but this has not been forthcoming up to the present.

In the case of protracted blight attacks late in the season it is important to distinguish between tubers in which the disease appears at, or soon after, the time of digging and those which develop disease some time after having been stored. Both outbreaks are often similarly explained (or, rather, are not distinguished), it being held that infection is in all instances contracted while the tubers are still *in situ* in the soil. At other times the appearance of large amounts of disease some time after digging is explained by the assumption that the disease spreads from tubers originally infected in the field to their neighbours during storage in pits and other places.

Evidence will be presented to show that the great bulk of the tubers which develop Phytophthora rot subsequent to digging were not already infected in the soil while still attached to the plant, and do not become infected in storage from contact with other tubers so attacked, but that, in fact, a distinction must be drawn between the ordinary course of infection (which may be called "subterranean infection") and another method, which, for want of a better term, may be called "surface infection." The distinction is, theoretically, not very far-reaching, but for practical purposes it is of much importance.

III.—Tuber Disease in Canada following Early Cessation of Spraying.

A further opportunity occurred in 1917 of testing the conclusion arrived at two years before, namely, that any circumstance which preserves the foliage until late in the season but then allows it to become partially blighted increases the amount of disease in the tubers. Owing to conditions over which sufficient control was not possible, a succession of sprayings was concluded nearly one month before the normal time on an experimental area of one acre of potatoes. The field was divided into twelve plots, of which three received no treatment, three were sprayed four times, three others three times, two plots twice, and one once. It was intended that certain of the plots should receive two further applications, but these were omitted. After spraying operations ceased the blight became serious, but the haulms in all the plots survived in part until October 3rd, when the potatoes were dug. The control plots were an exception, for they were most severely blighted and had been practically dead for some time. The results are given in Table I.

TABLE I.

Development of Phytophthora rot in sprayed and unsprayed potatoes in Prince Edward Island, Canada.

No. of applications of spray.	Percentage by weight of blighted tubers.			
	In the field.	In storage to Nov. 30.	In storage to April.	Total.
4	1·6	13·0	0·4	15·0
3	1·9	23·0	2·4	27·3
0	7·2	4·8	0·0	12·0
2	3·3	12·0	0·3	15·6
1	6·0	10·5	0·0	16·5
0	3·2	3·3	0·3	6·8
4	1·0	10·8	2·9	14·7
4	2·1	21·2	0·0	23·3
0	9·6	4·6	0·0	14·2
3	3·7	11·7	0·7	16·1
3	3·7	17·0	3·0	23·7
2	5·7	8·7	0·0	14·4
Average sprayed,	3·2	14·2	1·1	18·5
Average unsprayed,	6·7	4·2	0·1	11·0

It is evident that the sprayed plots (which, incidentally, gave an increased yield) showed a considerable reduction in the amount of diseased tubers, the average for the untreated plots being 6·7 per cent., and that for all the sprayed plots 3·2 per cent. The crop from each plot was placed separately in a storage cellar, and the potatoes were again sorted at the end of November. The result was then reversed, the potatoes from the sprayed plots showing on the average more than three times as much disease as those which had no treatment. This result was comparatively uniform throughout all the twelve plots, and, on the whole, the potatoes which were sprayed oftenest had the greatest amount of tuber rot, those sprayed less often had less, and the unsprayed plots had considerably the least. So great was the amount of disease which appeared after the potatoes were stored that it much more than neutralized the original advantage (so far as tuber disease is concerned) resulting from spraying.

A practically identical result was obtained from another acre plot in the same year (1917) which had similar treatment. The two last applications of spray had to be omitted on half the field (four plots), while the other four plots, which alternated with the first, were left untreated. There were somewhat more diseased tubers in the unsprayed plots when the crop was dug, but relatively much less after it was stored. The figures available give the amount of disease up to November 30th only, when the total for the unsprayed potatoes amounted to 12·7 per cent., while that for the sprayed potatoes reached 27·7 per cent.

These results seemed again to show that more tuber disease might follow a less severe, if more protracted, attack of blight. An examination of the results does not, however, support the view that the amount of tuber rot is a function of the length of the period of spore production.

The sprayed plots in which the disease lasted longest on the foliage showed the smallest amount of disease in the tubers at the time when the crop was dug. On the other hand, the potatoes from these plots developed a far greater percentage of the disease during the subsequent two months' storage. It is possible that the disease which became evident some time after digging was contracted before that operation, but that the rot had not advanced sufficiently to be visible. A direct answer to this objection cannot be given, because, unfortunately, the interval which elapsed between digging and the advent of the bulk of the tuber disease is not known. The supposition, however, is an improbable one.

When a potato tuber becomes infected with blight, visible evidence of infection under field conditions appears in about a week. That being so, all the disease is visible on potatoes dug on any particular date except that contracted, approximately, during the previous seven days. When, as frequently happens, a serious outbreak of tuber disease follows at an interval after harvesting, it presupposes, if this hypothesis be tenable, a remarkable increase in the amount of infection in the week immediately previous to digging—an increase which is difficult to explain. There is no evidence to support the suggestion of Jones and Morse,[1] that early digging favours the *development* of the parasite in the tubers, with the result that rot follows, while in the case of potatoes dug later the fungus, though present, remains dormant.

On the other hand, the great increase in the amount of tuber rot following after harvesting may, perhaps, be more reasonably connected with the changed

[1] Jones, L. R., and W. J. Morse: "The Relation of Date of Digging Potatoes to the Development of the Rot." Proc. 25th Ann. Meeting of Soc. for Promotion of Agricultural Science, pp. 91–95. 1904.

conditions as regards exposure to infection brought about by the actual lifting of the crop. To attempt to decide between these alternatives, three series of experiments were carried out in the subsequent two years.

IV.—Field Experiments on the Sources of Tuber Infection in Canada.

In an experiment carried out in 1918 the theory that storage rot originates from the contact of tubers with diseased foliage, or with surface soil within five days after it becomes contaminated, was tested in two ways. The stalks, then somewhat blighted, were removed from certain plots and the potatoes were not dug until a period of five days in one case, and eleven days in another, had elapsed. Other plots in which the foliage had been allowed to remain were dug at the same time. The second test devised consisted of digging two series of plots while the leaves were considerably blighted, and immediately treating the potatoes from one series with dilute formaldehyde solution so as to prevent further infection. All the plots were laid out in duplicate.

It is not necessary to go into the details of this experiment here, since the results were inconclusive for a number of reasons. The formaldehyde treatment, from which much was hoped, was apparently too drastic; for serious injury to the tubers, involving complications in decay, resulted. Furthermore, neither interval which was allowed between the removal of the stalks and the digging of the crop (five and eleven days) prevented a large amount of blight rot in storage. If there was anything in soil infection, it seemed as though a longer period must be allowed to elapse to render the crop safe. On the whole, however, the work appeared to be on the right lines. There was least disease in the potatoes treated with formaldehyde, and most in the tubers from those plots which were dug early and while the foliage was still blighted.

Profiting by this experience, two modified experiments were conducted in 1919. These are referred to as experiments A and B. In experiment A the efficacy of leaving a period of six days between the removal of the stalks and the digging of the crop was tested. In experiment B a much longer period was allowed—namely, thirty-four days. One experiment was carried out in quadruplicate and the other in triplicate. The average results are shown in Tables II and III.

TABLE II.

Experiment A (1919) *on the digging of potatoes at the Experimental Station, Charlottetown, Prince Edward Island, Canada.*

Plot.	Stalks allowed to stand until— (represented by ———)	Potatoes left undug until— (represented by .....)	Remarks.	Percentage weight of crop blighted.			Net weight sound potatoes in Nov. Avg., 4 plots. lb.
				In field.	To Nov., 1919.	Total.	
—	Date of Digging, Sept. 20 / Sept. 24 / Sept. 30 / Oct. 1 / Oct. 21		—	—	—	—	—
1	———	.....	—	0·0	35·4	35·4	69
2	———	.....	—	0·0	4·0	4·0	112
3	———	———	Stored at once.	0·0	40·4	40·4	76
4	———	———	Tubers left on ground all day.	0·0	68·3	68·3	42
7	———	———	Dug after frost: stored at once.	26·7	17·1	43·8	72
8	———	———	Tubers left on ground all day.	23·1	21·6	44·7	66

TABLE III.

Experiment B (1919) *on the digging of potatoes at the Experimental Station, Charlottetown, Prince Edward Island, Canada.*

Plot.	Stalks allowed to stand until— (represented by ———)	Potatoes left undug until— (represented by .....)	Remarks.	Percentage weight of crop blighted.			Net weight sound potatoes in Nov. Avg., 3 plots. lb.
				In field.	To Nov., 1919.	Total.	
—	Date of Digging, Sept. 18. / Sept. 27. / Oct. 22.		—	—	—	—	—
1	———	———	Tubers buried in soil again.	8·7	5·9	14·6	89
2	———	.....	—	4·7	3·3	8·0	118
3	———	.....	Soil sprayed: Bordeaux mixture	3·7	2·4	6·1	113
4	———	.....	—	.....[1]	21·7	21·7	104
5	———	———	—	0·0	35·6	35·6	91
6	———	———	Dug after frost.	11·9	3·9	15·8	123

[1] A very small amount of disease found in the tubers in the field was not recorded separately, but it is included in the total.

It is clear from the first table that removing the stalks six days before harvesting is of little avail in preventing tuber infection (compare plots 1 and 3). This is so in spite of the fact that removing the stalks on September 24th reduced the length of the blight attack on the foliage by one-third. Removing the stalks ten days before digging reduced tuber infection to very small proportions. Here again, of course, the period during which blight was present on the foliage was still further diminished. It is probable that a considerable share of the success attained was due to this fact. The exact influence of each of the two factors cannot be apportioned, but it may be mentioned that a large amount of tuber infection resulted from allowing eleven days to elapse between stalk removal and digging in the experiment of 1918; and also a large amount of infection occurred in experiment B of 1919, where the interval was nine days. Ten days elapsed in the case under discussion, and while it is true that the weather conditions (which must probably be allowed to have an influence) differed in the different cases, the protection afforded to the crop is to be traced principally to the initial amount of blight present and not to the interval allowed before digging.[1]

Turning to experiment B, clear proof is obtained of the origin of Phytophthora rot in storage. The plants in plots 2, 4, and 5 retained their foliage until September 18th, when they were all moderately blighted. The last-mentioned plot was then dug at once, and the crop stored on the same day. The plants in the second and fourth plots had all their foliage removed, and one was dug nine days and the other thirty-four days later. It will be noted that the period of the blight attack was the same length in all. Notwithstanding this, 35·6 per cent. of the tubers from the early-dug plot had developed blight by November, 21·7 per cent. from the intermediate one, and 8·0 per cent. from the late-dug plot. It seems impossible to escape from the conclusion that during the thirty-four-day interval the parasite lost its power of infecting the tubers, but that, on the other hand, this power persisted for at least nine days after the last spore was shed from the leaves.

As was invariably the rule in all the experiments, three in Canada and one in Ireland, the greatest amount of tuber rot developed when the crop was dug while the foliage was still suffering from blight. On the one hand this compares with a smaller amount of disease in plots, the stalks in which were removed at or about the same time as the former were dug, but the crops of which were not dug until at least two weeks later; and, on the other

[1] This and other points, such as the possibility of the soil of plots from which the stalks had been removed being contaminated by spores from neighbouring plots, and the possibility of tuber infection during storage, are discussed more fully in a forthcoming Bulletin of the Dominion of Canada Department of Agriculture, entitled "Investigations on Potato Diseases."

hand, with plots dug in the ordinary way late in the season. This is a very noteworthy point. That potatoes which were left in the ground exposed to blight infection from spores washed down into the soil for an added period varying from twenty-one to thirty-four days should decay less than potatoes not so exposed points to some incompleteness in the generally accepted theory of tuber infection.

V.—Field Experiment on the Sources of Tuber Infection in Ireland.

In view of these results it was thought advisable to try a similar experiment in Ireland. While it is probably true that storage rot is seldom, if ever, as severe in this country as in portions of Eastern Canada, nevertheless loss due to this cause is hardly ever absent, and in some cases it becomes quite serious.

Portion of a field of Up-to-Date potatoes at the Albert Agricultural College, Glasnevin, Dublin, measuring twenty-five square perches, was selected for the work. This area was divided into thirty-three equal plots. Each of the eleven methods of treatment indicated in Table IV was tried in triplicate on these plots, which were distributed as uniformly as possible over the experimental area so as to minimize inequalities in the blight and soil conditions. Different treatments were given before and after digging, as detailed in the table, the dates of digging being there indicated. Before being stored, the potatoes were most carefully sorted and all diseased and small tubers excluded (except in the case of plot 8). The remainder were stored in small pits in the open. Each pit contained about 2½ cwt. of potatoes, representing the yield of each series of three plots. The pits were made in the usual way, very slightly sunk in the ground, the potatoes being covered lightly with straw, or, in certain cases, with potato stalks. Where old stalks were purposely used for covering they were replaced with straw after a few days. All the pits were finally covered with earth. They were opened and the potatoes again examined on February 15th and 16th, 1921.

[Table IV.

TABLE IV.

Digging and pitting experiment at the Albert Agricultural College, 1920–21.

Plot.	Stalks allowed to stand until— (represented by ———)			Potatoes left undug until— (represented by .....)		Special treatment after digging (if any).	Per cent. weight found rotted when pits were opened.	
—	Date of Digging, Sept. 15, 16	Sept. 27, 28	Oct. 9, 12	Oct. 18			Soft rot (cause undetermined).	Blight.
1	———					None.	1·05	3·86
2	———	———				None.	0	0·68
3	———	———	———			None.	0·16	9·60
4	———	———	———	———		None.	1·16	10·04
5	———	·····				None.	1·07	0·27
6	———	———	·····			None.	0	0·10
7	———	———	———	———	·····	None.	0	0·63
8	———					Covered in pit with blighted stalks.	0·33	13·16
9	———	·····				Covered in pit with blighted stalks.	0·81	9·76
10	———	·····	·····			Pitted with fifty marked blighted tubers.	1·71	0·85
11	———	·····	·····	·····	·····	Spread on plot from which blighted stalks had just been removed.	0·66	0·33

The field in which the plots were situated had suffered severely from blight throughout the latter part of July and the month of August. By the beginning of September the plants in more than half of the field were practically dead, and those in the remainder were severely blighted, but still living vigorously. The experiment was carried out on this portion of the field.

The blight made little or no headway during the comparatively dry and warm period which set in about September 1st. It had progressed no further at the time of the first digging on September 15th and 16th; and it was not until just after the second digging on September 27th and 28th that, as the result of some showery weather, it began to spread again. Thereafter the disease continued to develop, although somewhat slowly, so that there was still a certain amount of living foliage left when work was completed on October 18th.

The potatoes reported as attacked by soft rot included those which were so far decayed that the original cause could not be determined. No effort at an analysis of this category was attempted because of its difficulty. Besides, the amount of this type of rot in all cases but one hardly exceeds one per cent., and the results are not materially altered by neglecting it altogether. In the case of plot 10, where it reaches its highest level, it is noteworthy that while fifty marked blighted tubers were placed in the pit only thirty-nine were recovered in a recognizable form. Some of these would have been included in the soft rot column had they not been marked. It is probable that the missing eleven are to be similarly accounted for. If this be true for the other plots also, all the rotted potatoes should be included in the blight column, in which case again no serious difference results.

Three points are clear from this experiment. The disease which was found when the pits were opened had not spread from a few initially infected tubers. The pit (No. 10) in which blighted potatoes were placed showed hardly more blight than did No. 6 pit, which contained similarly treated potatoes without the addition of any blighted specimens. There was little evidence of any disease being communicated from tuber to tuber. In most cases the potatoes surrounding the marked blighted tubers were quite sound, although in some cases the former were covered with decaying slime. It was exceptional to find marked diseased, and unmarked potatoes which had contracted disease, in contact. As the covering of the pit was not absolutely water-tight and the interior was moist, the conditions were presumably favourable for the development of blight.

The most dangerous source of infection is, according to the experiment, direct contact of the tubers with blighted foliage. Two pits were covered for some days with the blighted stalks, which were afterwards removed and replaced with straw. No. 8, which was so covered, developed 13·16 per cent. of disease, as compared with 3·86 per cent. in similarly treated, but differently covered, potatoes in pit 1, an increase of 9·3 per cent. A similar difference exists between pits 6 and 9. The latter, which was covered with diseased stalks, showed 9·76 per cent. of blight. The former, not so covered, showed 0·10 per cent., the difference being 9·66 per cent. in this case. Although it is well known that the leaves are the source of the spores which infect the tubers, the use of stalks as a temporary covering for freshly dug potatoes is still too common a practice, and, as the experiment shows, it is a most dangerous one. Had there been a vigorous development of blight on the leaves, the result would probably have been even more serious.

It is clear, in the third place, that direct and deliberate contact of the foliage and tubers is not necessary for the production of serious

storage rot. This is seen especially by comparing pits 3 and 6 and pits 4 and 7. The corresponding pairs of plots had been dug on the same dates, respectively. The difference consisted in that the foliage had been removed from one each of the two pairs twenty-five days and thirty-three days before digging, while it had not been removed from the other two. This operation brought about two changes in the conditions, either of which might, theoretically, be held accountable for the reduction in the disease. The duration of the blight attack on the foliage was reduced, on the one hand, and with it the supply of spores capable of being washed down to the tubers. On the other hand, the contamination of the soil ceased, and a period elapsed presumably sufficient for the spores present at or near the surface to lose their vitality.

It is not possible to apportion with certainty the exact influence of each of these two factors. This is because the blight, instead of diminishing gradually with the progressive death of the foliage, rallied from the low ebb it had reached about the middle of September (when the first and second diggings were done), and was more severe at the time of the third and fourth diggings. Had it not been so, it was anticipated that there would have been a gradual diminution in the amount of tuber disease found in storage in the series of plots from 1 to 4, and a still more marked diminution in the series 5 to 7. Furthermore, the lifting of plots 4 and 7 had to be hastened owing to the exigencies of farm operations, although it was intended that they should be left until well after the death of the foliage was complete. A reduced amount of tuber disease was again anticipated from this course.

While certainty was not attained, an examination of the evidence shows that the probabilities are in favour of the theory of infection at digging time. In support of this are the following points :—

(1) All the plots went through a very severe blight attack, lasting from the latter part of July until the end of August, with but slight injury to the tubers (as measured by the amount of disease found in them when dug), at a time when they were immature, and theoretically more susceptible to infection.

(2) The amount of blight found in the tubers in the field was slight and, comparatively speaking, uniform ; and it did not vary directly with the date of digging or with the length of the period during which the foliage was allowed to stand. The variations were irregular, though not of great magnitude. The highest total of disease in the field was found in one of the plots dug first, and the next highest in one dug nearly last,

(3) The amount of blight appearing in the tubers in storage, generally speaking, stands in relation to the amount of blight present at and previous to the time of digging.

(4) The general appearance of an increased amount of disease in the crop, which is not visible at the time of harvesting, but becomes so some time afterwards, and which must be due to infection soon before or when the crop is being lifted, can be related to no change in the conditions regularly occurring before digging, but must more probably be referred to the change brought about by that operation itself.

It is not necessary to labour these points. The experiment points generally in the same direction as the series carried out in Canada, and proves that potatoes may become heavily infected with blight when they are brought into contact or close relationship either with diseased stalks or contaminated surface soil. The former possibility will be generally admitted as a danger, as the result of the work of Jensen, Jones and Morse, and the present author. The view that the latter is a serious and hitherto largely unsuspected source of infection is strongly supported by evidence based on laboratory studies of the behaviour of the spores under varying conditions of environment which have been made during the past winter, an account of which will be given in a separate communication.

SUMMARY.

Evidence is presented that more Phytophthora tuber disease may follow a less severe attack of foliage blight, occurring late in the season, than results from a severe outbreak which runs a rapid course.

Conditions favourable to tuber infection may be brought about in Eastern Canada, or elsewhere if the circumstances are similar, if potatoes are sprayed in the early part of the season, but left untreated towards the later portions.

Under such circumstances it is important to distinguish between the disease which appears in the tubers at or very soon after lifting and that which appears some time later. It is the later development of the disease which becomes serious following protracted or late outbreaks of blight.

Evidence derived from field experiments in Canada and in Ireland is presented to show that the bulk of the infection in the case of potatoes which develop blight in storage is contracted when the tubers are being dug.

It is shown that direct contact of the tubers with partially blighted foliage results in serious rot in storage.

The blight does not spread from tuber to tuber even in moist pits to any considerable extent, if at all.

Soil contaminated by means of spores shed from the leaves continues capable of inducing blight in freshly dug tubers which are brought into contact with it over a period of at least ten days, and probably longer.

The part played by contaminated soil is fully established by the results obtained in laboratory investigations, which will be published separately.

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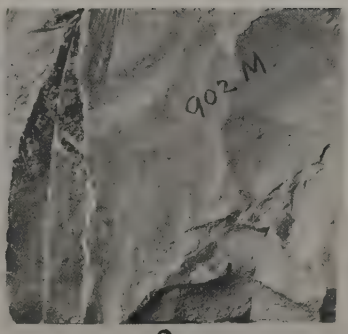

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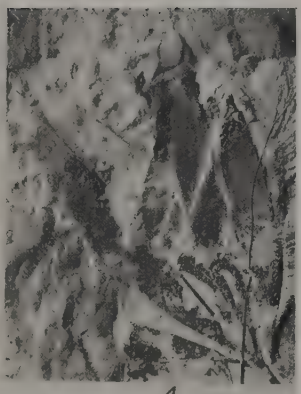

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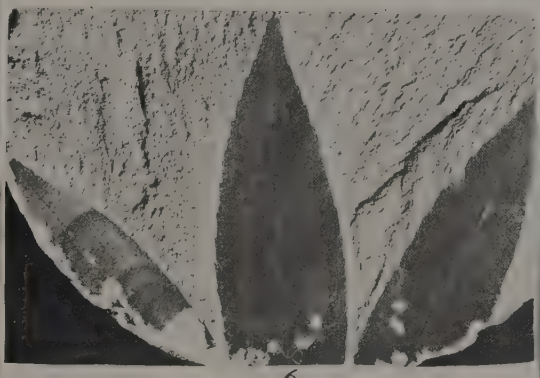

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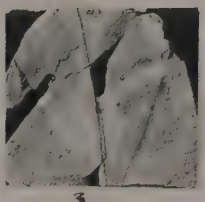

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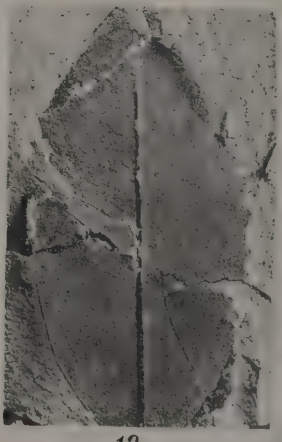

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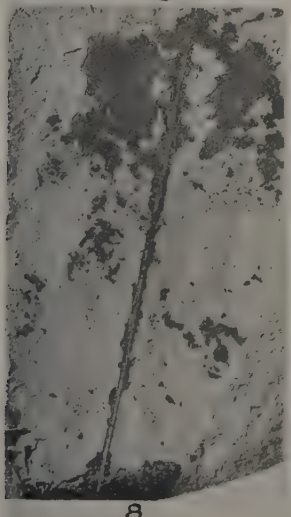

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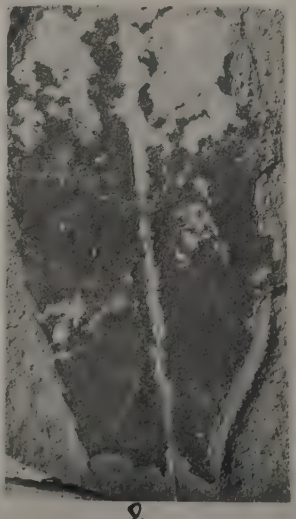

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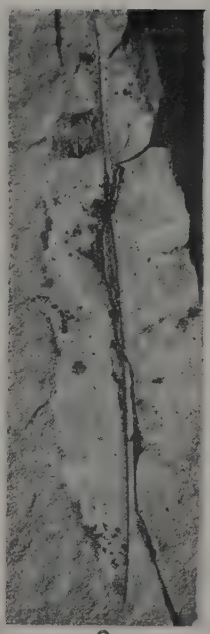

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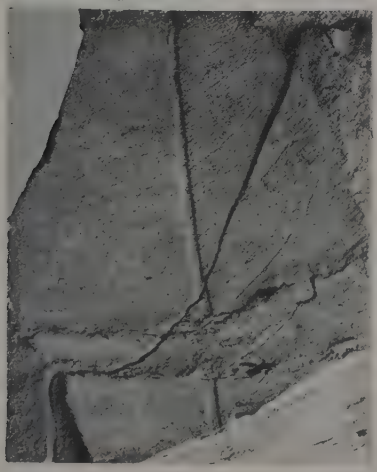

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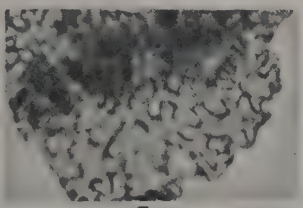

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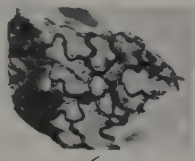

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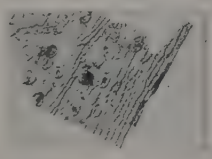

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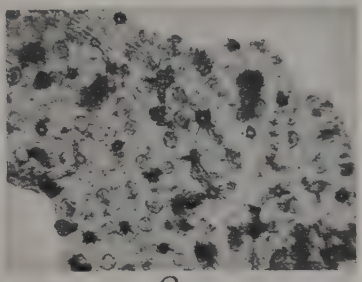

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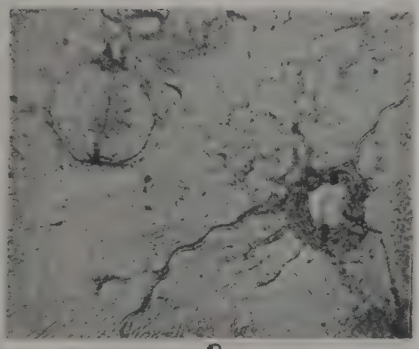

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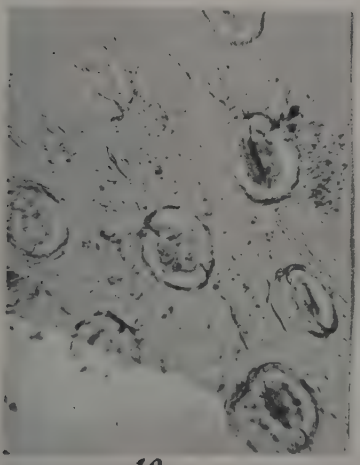

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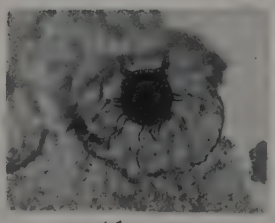

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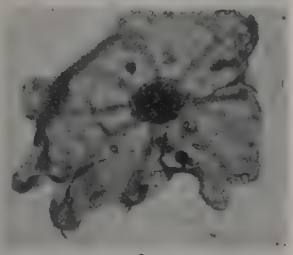

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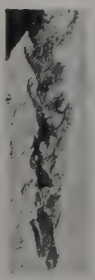

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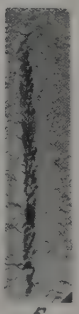

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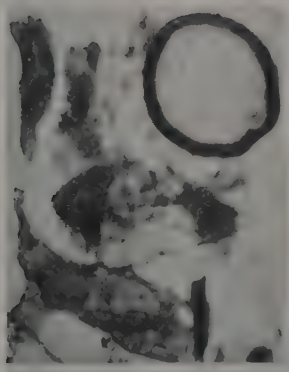

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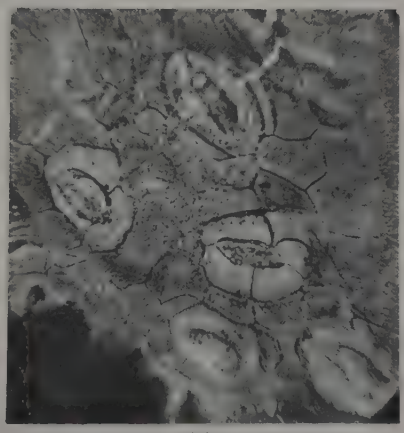

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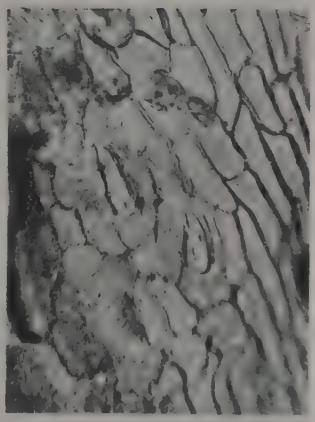

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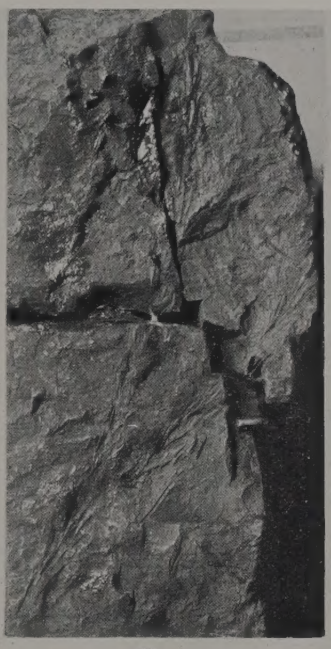

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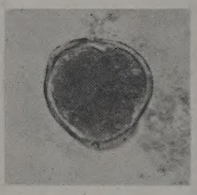

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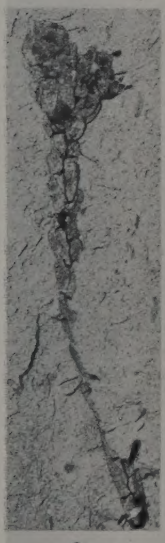

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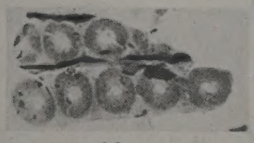

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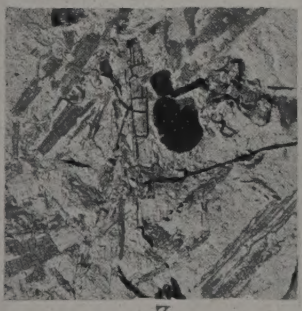

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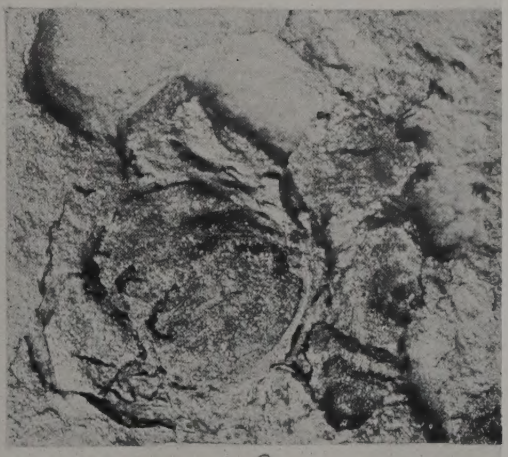

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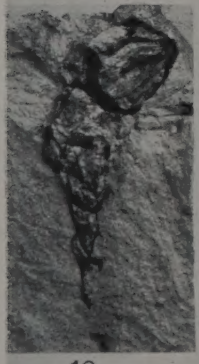

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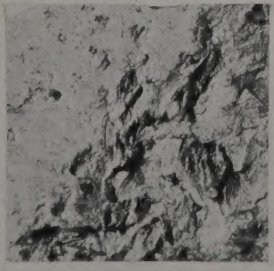

12

13

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